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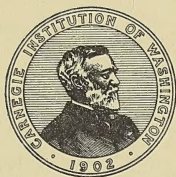
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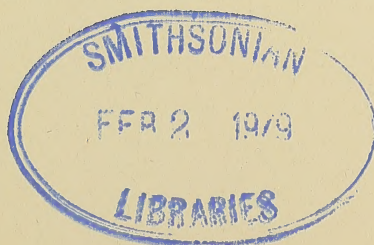
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I

GASTEROSTOMES (TREMATODA) OF TORTUGAS, FLORIDA

By Harold W. Manter

University of Nebraska

With twenty-six figures

GASTEROSTOMES (TREMATODA) OF TORTUGAS, FLORIDA

This paper is a report on the gasterostomatous trematodes collected by the author at the Marine Biological Laboratory of the Carnegie Institution of Washington at Tortugas, Florida during the summers of 1930, 1931, and 1932. Included among the 15 species are 3 species described in an earlier publication (Manter, 1934) from deep-water fishes. Linton (1910, pp. 79-81) reported 4 "Gasterostomum sp." from Tortugas. While his descriptions are incomplete, all the species with which he was dealing are thought to be represented in the present collection and are identified as follows. Linton's first "Gasterostomum sp." is *Doliffus-trema gravidum*, his second and third are *Prosorhynchus atlanticus*, and his fourth is a mixture of *Bucephalopsis dolichoon* and *B. arcuatus* (Linton). Not included in this paper is the immature *Dolichoenterum* sp. reported from *Citharichthys cornutus* by Manter (1934, p. 271).

Of these 15 species of gasterostome, 9 are considered new, although 3 of these 9 were partially indicated (but unnamed) by Linton (1910). Two species (*Bucephalus varicus* and *Prosorhynchus ozakii*) are known from the tropical American Pacific, and 2 (*Rhipidocotyle baculum* and *Bucephalopsis arcuatus*) are known from Beaufort, North Carolina. *Bucephalopsis arcuatus* is also known from Woods Hole, Massachusetts.

No general account of the Gasterostomata will be attempted here. Several recent reviews of this group are available (Nagaty, 1937; Eckmann, 1932; Verma, 1936; Manter, 1940).

All measurements in this paper are in millimeters unless microns are indicated.

Type specimens are deposited in the United States National Museum.

GASTEROSTOMATA Odhner, 1905

BUCEPHALIDAE Poche, 1907

Bucephalus varicus Manter, 1940

Synonym. *B. polymorphus* Nagaty, 1937

Hosts. *Caranx bartholomaei* Cuv. & Val. (in 1 of 2)

C. latus Agassiz (in 1 of 6)

C. ruber (Bloch) (in 5 of 6)

Location. Stomach and intestine

The above records were reported by the author (Manter, 1940, p. 335), who collected the same species from *Caranx* species in the Pacific.

Bucephalus priacanthi, n. sp.

(Figures 1, 2)

Host. *Priacanthus arenatus* (Lacépède)*Location.* Intestine*Frequency.* 7 to 10 specimens from 1 of 3 hosts

Diagnosis. Body elongate, tapering anteriorly, broadly rounded posteriorly, widest near posterior end, length 1.020 to 1.215, width 0.210 to 0.285. Anterior sucker with 7 large tentacles (extended in all specimens collected), each with a large basal process or prong and near it a smaller, more distal prong (fig. 2). In a 1.080-long specimen, a tentacle with recurved tip measured 0.094 over all and 0.043 from base to basal prong. Mouth near or slightly posterior to midbody, opposite ovary or anterior testis; pharynx usually longer than wide, 54 to 60 microns long, 41 to 58 microns wide; intestine saclike, extending slightly anterior and posterior to pharynx. Gonads large, tandem, close together. Ovary subtriangular, pretesticular, about in midbody, opposite pharynx. Vitelline follicles in two separate, lateral groups extending from level of ovary halfway or more to anterior end, partly covered by uterus. Vitelline ducts uniting near anterior border of posterior testis. Uterus extending anteriorly almost to base of anterior sucker, filling most of body, extending posterior to genital pore. Eggs yellow, 17 to 19 by 10 to 12 microns.

Testes large, globular, tandem or slightly diagonal, close together. Cirrus sac overlapping posterior testis. Genital pore near posterior end of body. Excretory vesicle extending to base of anterior sucker.

Measurements of type specimen (fig. 1) are: length, 1.110; width, 0.285; diameter of anterior sucker, 0.900; mouth to anterior end, 0.562; diameter of pharynx, 0.060; cirrus sac, 0.300 by 0.085.

Comparisons. This species is most similar to *B. varicus*, with which it may possibly be identical. Difficulties of comparison arise from the variations observed in *B. varicus*. *Bucephalus priacanthi* (judging from agreements in 7 specimens) has a different shape, being wider and more broadly rounded posteriorly; the uterus extends farther anteriorly, reaching either to or almost to the anterior sucker; the excretory vesicle reaches to the anterior sucker, and the tentacles are relatively larger than in the *B. varicus* collected from either the Atlantic or the Pacific. It differs from Nagaty's specimens of *B. varicus* in still more marked anterior extent of the uterus.

Bucephalus scorpaenae, n. sp.

(Figures 3, 5)

Host. *Scorpaena plumieri* Bloch*Location.* Intestine and ceca*Frequency.* Present in 3 of 3 hosts examined

Diagnosis (based on a study of 29 specimens). Body more or less cylindrical; when extended the length is 7 or 8 times the width, when contracted the width is about 4 times the length. Measurements on 7 specimens are: length 2.065 to 2.792 by 0.300 to 0.337. Another somewhat contracted specimen measured 1.685 by 0.435. Anterior sucker (fig. 4) 0.150 to 0.165 in diameter with 7 conspicuous, similar tentacles, each with a single basal prong. Dorsal wall of sucker somewhat vesicular, probably glandular. Pharynx either at midbody or slightly anterior or posterior to midbody. Intestine short, extending posterior to pharynx. Gonads approximately tandem, to the right, immediately posterior to intestine. Ovary globular, close to or partly overlapping intestine, pre-testicular. Vitelline follicles spherical, arranged in two almost linear lateral rows extending from level of pharynx just about halfway to anterior end of body; 12 to 16 follicles on each side; yolk duct extends backward to near posterior testis, then, forming a loop, bends anteriorly to be joined by the other duct, the common yolk duct entering oviduct between ovary and testes. Uterus extending backward to posterior testis, then forward well anterior to vitellaria but not to anterior sucker, then backward to genital atrium. Eggs yellow-brown, broadly rounded at one end, 19 to 22 by 13 to 15 microns.

Testes globular, close together, anterior testis usually separated from ovary by a short space. Cirrus sac rather slender, to the left, overlapping posterior testis, containing an elongate-oval seminal vesicle, prostate gland, and male tube. Three regions of about equal length can be seen in the male tube: a basal region of the pars prostatica with tall, narrow cells; a median region of the pars prostatica with papillae; and a smooth-walled ejaculatory duct. Genital atrium (fig. 5) large, somewhat wider than cirrus sac, with rounded dorsal genital lobe with nipple-shaped prolongation. Uterus connected with genital atrium by a narrow thin-walled tube surrounded by gland cells. This tube (which may be called the *uterine tube*) enters the atrium dorsally close to but not at its anterior border. Atrium connected to genital pore by a short atrial duct. Genital pore near posterior end of body, ventral or sub-

ventral. Excretory pore terminal, dorsal to genital pore. Excretory vesicle extending to near the anterior limit of the uterus, rarely extending anterior to uterus but not reaching close to anterior sucker.

The name *scorpaenae* is for the host.

Comparisons. In having a single basal prong on the tentacle, *B. scorpaenae* is unlike *B. elegans* Woodhead and *B. uranoscopi* Yamaguti. It is surprisingly similar to *B. polymorphus* (Baer) as redescribed by Eckmann, 1932. It has similar tentacular processes, similar extent of uterus, and similar position of mouth and generally of gonads. *Bucephalus polymorphus* however, is smaller in size (length only 0.8 mm.) and has markedly longer eggs (26 by 15 microns as compared with 20 by 14 microns). There seem to be other differences, especially in the size and shape of the genital atrium and the relative diameter of the testes. *Bucephalus scorpaenae* differs from *B. priacanthi* in less anterior extent of the excretory vesicle and uterus, in lacking a second tentacular prong, in wider genital atrium, and in body shape. A comparison of 29 specimens of *B. scorpaenae* with the *B. varicus* of the author (Manter, 1940) shows a number of constant differences: the body is considerably larger, the uterus never extends posterior to the genital atrium, the tentacles have a single prong, the excretory vesicle only rarely extends anterior to the uterus, the gonads are almost always smaller, and the mouth is almost always more anterior. The most conspicuous of these differences is the posterior extent of the uterus. The tendency toward specificity among gasterostomes suggests a note that the hosts are different.

Bucephalus scorpaenae seems to be restricted to *Scorpaena plumieri*. While it was collected from each of 3 specimens of this host examined, it was not collected from 6 *S. agassiz*, 5 *S. brasiliense*, 2 *S. grandicornis*, or 2 *S. inermis*.

Bucephalus kathetostomae (Manter, 1934) Manter, 1940

Synonym. *Rhipidocotyle kathetostomae* Manter, 1934

Host. *Kathetostoma albigutta* Bean

Location. Intestine

Frequency. Present in 2 of 3 hosts examined

This species is reported by Manter (1934, p. 269) from a depth of 60 fathoms.

Rhipidocotyle nagaty, n. sp.

(Figure 6)

Host. *Euthynnus alletteratus* (Raf.)

Location. Intestine

Frequency. Collected from 3 of 3 hosts examined

Diagnosis (based on 9 specimens). Body more or less flattened, width usually about $1/3$ length; size 1.593 to 2.241 by 0.487 to 0.675; widest at about the level of the pharynx somewhat anterior to midbody. Preoral portion of body not narrowed. Truncate anterior end with a conspicuous, distinctly pentagonal, muscular "hood" or cephalic disc. Disc deeply notched at mid-ventral line with a pair of median-ventral lobes thickened medianly on the under side. Disc more or less pointed laterally on each side and at a median dorsal point. Median dorsal lobe with an internal strip of granular tissue. Anterior sucker 0.105 to 0.202 in diameter. Cephalic disc 0.277 to 0.338 in diameter. Pharynx spherical, slightly anterior to midbody, 0.105 to 0.133 in diameter. Intestine short, tubelike or inflated, extending posteriorly to overlap anterior testis.

Gonads close together, more or less in line, either almost tandem or definitely diagonal. Ovary subglobular, smooth or slightly irregular in outline, pretesticular, to the right, posterior to pharynx, lateral to intestine. Vitelline follicles large, distinct, more or less lobed or irregular in outline, 12 to 18 on each side forming two separated, lateral clusters from posterior edge of pharynx somewhat less than halfway to anterior sucker. Anterior to pharynx the follicles extend somewhat medianly but do not meet. Vitelline ducts uniting between testes or lateral to anterior testis, in which case one duct runs between testes. Seminal receptacle small, postovarian. Coils of uterus chiefly longitudinal, not extending anterior to pharynx or posterior to genital atrium. Eggs ovoid, broadly rounded at each end, 17 to 27 by 10 to 18 microns. However, within any one specimen the size range is small (e.g., 17 to 18 by 11 to 12 microns; 22 to 25 by 15 to 17 microns; 25 to 27 by 17 to 18 microns).

Testes closely posterior to ovary, slightly or markedly diagonal, extended diagonally. Cirrus sac rather slender, reaching anterior to or almost to posterior testis, which it may overlap; containing a small ovoid seminal vesicle and sinuous pars prostatica. Two genital lobes, more or less right and left; the left lobe very much larger, rather irregular in shape, more or less filling genital atrium. Genital pore ventral, a short distance anterior to posterior end of body. Excretory pore terminal; vesicle extending to posterior edge of pharynx.

The species is named for Professor H. F. Nagaty.

Comparisons. The pentagonal shape of the cephalic disc without papillae separates *R. nagaty* from other species in the genus except *R. pentagonum*. It differs from *R. pentagonum* in its wider body, more diagonal gonads, less linear arrangement of the vitelline follicles, relatively larger pharynx, more longitudinal uterine coils, and deeper median cleft of the cephalic disc.

Rhipidocotyle barracudae, n. sp.

(Figures 7, 8)

Host. *Sphyræna barracuda* (Linn.)*Location.* Intestine and ceca*Frequency.* Identified in 2 of 15 hosts examined; frequency probably greater

Diagnosis. Body elongate, 1.207 to 1.782 by 0.240 to 0.547; anterior half flat, thin and more narrow, without organs, posterior half plump, cylindrical, thick and wide, containing reproductive organs (body form similar to that of *R. baculum*). Anterior sucker slightly wider than long, 0.093 to 0.120 in transverse diameter, cephalic disc 0.157 to 0.180 in diameter, with 5 lobes (2 ventral, 2 lateral, and 1 dorsal); 2 ventral lobes separated by a broad indentation. Mouth almost always slightly posterior to midbody (exactly in midbody in 1 specimen); **pharynx** suckerlike, subspherical, large, 0.078 to 0.119 in diameter; esophagus extending dorsally and anteriorly; intestine saclike, extending posteriorly (in all of 10 specimens the intestine reached posterior to the ovary and in 9 of 10 specimens it reached to or almost to the cirrus sac). Gonads contiguous, either tandem or crowded together almost at the same level. Ovary to the right, pretesticular, immediately posterior to pharynx. Vitelline follicles in two separated clusters extending from level of pharynx only a short distance anterior to midbody; usually 12 to 15 follicles on each side. Uterus not extending anterior to vitellaria, filling most of posterior half of body, extending posterior to genital pore; eggs 27 to 31 by 10 to 17 microns.

Testes tandem or oblique, close together. Cirrus sac 0.352 to 0.435 long by 0.087 to 0.112 wide, overlapping posterior testis, extending to the anterior testis; seminal vesicle subspherical; genital atrium rather long, genital lobes weak; genital pore near posterior end of body. Excretory pore terminal; excretory vesicle extending forward to middle of vitelline field, not anterior to vitellaria.

The name *barracudae* is for the host.

One specimen was infected by some very minute microorganism filling the parenchyma in the pharynx region.

Comparisons. This species differs from most members of the genus in its 5-lobed cephalic disc without papillae. It has a body form similar to that of *R. baculum*, but differs in larger size and much larger eggs. It differs from *R. pentagonum* in more posterior extent of intestine, less anterior extent of vitellaria, more anterior extent of excretory vesicle and uterus, and larger eggs. It differs from *R. nagaty* in shape of body, more posterior vitellaria, broader ventral indentation of disc, in lacking markedly longitudinal coils, and in larger eggs.

Rhipidocotyle longleyi Manter, 1934

Host. *Hypoclydonia bella* Goode & Bean

Location. Intestine

Frequency. Present in 5 of 17 hosts examined

This species is reported by Manter (1934, p. 267) from depths varying from 140 to 250 fathoms.

Rhipidocotyle adbaculum, n. sp.

(Figures 9-12)

Host. *Scomberomorus regalis* (Bloch)

Location. Intestine

Frequency. Present in 1 of 3 hosts examined

Diagnosis. Body elongate, 1.215 to 1.620 by 0.232 to 0.300. Anterior sucker 0.090 to 0.120 in diameter, with a conspicuous cephalic disc noticeably wider than anterior end of body, 0.160 to 0.190 in diameter (fig. 10). Dorsal and two ventral lobes of disc well marked, lateral edges rounded. Mouth usually slightly anterior to midbody in 2 specimens; pharynx 0.041 to 0.053 in diameter; intestine short, saclike, extending posteriorly.

Gonads more or less tandem immediately posterior to mouth. Ovary globular, pretesticular, to the right and partly overlapping anterior testis; seminal receptacle small; Mehlis' gland just posterior to ovary, opposite anterior testis or between testes. Vitelline follicles in two lateral, separated groups extending from level of pharynx only a short distance anteriorly, each group with 12 to 17 follicles approaching the other group medianly but not meeting. Uterus filling most of body posterior to mouth (in 1 of 17 specimens the uterus barely reached beyond the mouth, extending posterior to genital pore; eggs thin-shelled, 15 to 17 by 9 to 10 microns.

Testes globular, tandem or slightly diagonal, in contact or not far apart. Cirrus sac extending forward to posterior or anterior testis, containing a subspherical seminal vesicle and a long, straight or slightly curved pars prostatica with tall cells; genital atrium with one large and a smaller tri-papillated genital lobe; atrium duct muscular, variable in length; genital pore a short distance anterior to posterior end of body. Excretory pore terminal; anterior extent of vesicle not determined.

The name *adbaculum* indicates similarity to *R. baculum*.

Comparisons. *R. adbaculum* can be distinguished from *R. baculum* by the size and shape of the cephalic disc (figs. 10, 11), which in *R. adbaculum* is larger and has a dorsal point. The body is larger and more

elongate. *Rhipidocotyle adbaculum* differs from *R. barracudae* in more slender body, much smaller pharynx, and much smaller eggs. It differs from *R. nagaty* in body form, in location of vitellaria and pharynx, and in uterine coils.

Rhipidocotyle baculum (Linton, 1905) Eckmann, 1932

Synonyms. *Gasterostomum baculum* Linton, 1905

Gasterostomum sp. Linton, 1901 from *Scomberomorus maculatus*

Nannoenterum baculum (Linton)

Host. *Scomberomorus regalis* ?

Frequency. Collected once from a single mackerel the identification of which was uncertain

It seems very possible that this fish was actually *Scomberomorus maculatus*. *Rhipidocotyle baculum* has hitherto been known only from *S. maculatus*. On the other hand, the only gasterostome previously found in 3 specimens of *S. regalis* examined has been *R. adbaculum*.

Bucephalopsis longoviferus, n. sp.

(Figures 13, 14)

Synonym. *Gasterostomum* sp. Linton, 1910, pp. 80-81 (in part)

Host. *Sphyræna barracuda* (Linn.)

Location. Ceca and intestine

Frequency. 8 of 15 barracudas examined were infected with gasterostomes. Sometimes 3 species of gasterostome were present in a single fish. *Bucephalopsis longoviferus* was collected 4 times but because of its small size might have been overlooked in other cases.

Diagnosis. Body flattened; 0.630 to 1.050 by 0.112 to 0.262; greatest width (slightly anterior to midbody) about 1/4 length. Anterior sucker subcircular, 0.043 to 0.051 in transverse diameter. Mouth usually somewhat posterior to midbody, but may be almost at midbody, opposite ovary. Pharynx 0.036 to 0.041 in diameter; intestine ovoid, saclike, extending dorsally and anteriorly. Ovary nearly at midbody level, to the right. Vitelline follicles in two lateral, widely separated groups of 11 to 14 on each side, extending in second fourth of body length. Uterus extending anteriorly between vitellaria far forward almost to anterior sucker, posteriorly to or beyond the genital atrium. Eggs thin-shelled, elongate, 26 to 31 by 8 to 11 microns or approximately three times longer than wide. Testes globular, postovarial, oblique, separated by uterus. An-

terior testis diagonally posterior to ovary. Cirrus sac elongate, $1/3$ to $1/4$ body length, extending beyond posterior testis almost to anterior testis; seminal vesicle subspherical to ovoid; pars prostatica long. Genital atrium large; ventral genital lobe large, fingerlike; dorsal lobe divided into four parts (fig. 14). Genital pore ventral, inconspicuous, near posterior end of body. Excretory pore terminal; vesicle sometimes reaching only to mid-cirrus sac level, sometimes to the ovary.

The name *longoviferus* is from *longovi* = long egg and *ferus* = bearing.

Comparisons. This species differs from all others in the genus in the elongate shape of the egg, which has a width only $1/3$ its length. The relative extents of the uterus, vitellaria, and cirrus sac will also separate the species from others in the genus.

Bucephalopsis longoviferus was without doubt represented in the collections of "Gasterostomum sp." recorded by Linton (1910, pp. 80-81) from the barracuda. Linton recognized much diversity in his collections from this host, but his material was insufficient to separate species. His figure 24 is evidently *B. longoviferus*.

Bucephalopsis arcuatus (Linton, 1900) Eckmann, 1932

(Figures 15, 17)

Synonyms. *Gasterostomum arcuatum* Linton, 1900

Gasterostomum sp. Linton, 1910, pp. 80-81 (in part)

Host. *Sphyræna barracuda* (Linn.)

Location. Ceca and intestine

Frequency. Common

Diagnosis (based on numerous specimens). Length 0.667 to 1.444; width 0.232 to 0.375. In elongated specimens, width about $1/5$ length. Anterior sucker 0.053 to 0.066 in diameter. A slight thickening of the body at anterior edge of sucker. Mouth about at midbody; pharynx 0.046 to 0.053; intestine saclike, dorsal and anterior to pharynx. Ovary to the right, opposite or slightly posterior to pharynx. Vitelline follicles in two lateral, separated, more or less longitudinal rows, 12 to 16 on each side, from level of pharynx only a short distance anteriorly. Uterus extending anteriorly usually only to anterior edge of ovary, rarely to anterior limit of vitellaria; it may but usually does not extend posterior to genital atrium. Eggs 20 to 22 by 9 to 14 microns. Testes tandem or slightly diagonal, close together or slightly separated. Cirrus sac elongate, always extending beyond posterior border of posterior testis and sometimes reaching to pharynx (thus being at times about $1/2$ body length). Excretory pore terminal, vesicle extending to pharynx.

Several specimens had abnormal eggs of all sizes and shapes (fig. 17), some apparently masses of eggshell material empty of embryos. Linton's

(1910, p. 80) comments on unreliability of egg size in gasterostomes are probably due partly to such malformed eggs.

Comparisons. Eckmann (1932) could not separate *B. pusilla* (Staff.) and *B. arcuatus*. More recent figures of the former by Van Cleave and Mueller (1934) together with Woodhead's (1930) description show that *B. pusilla* is smaller with larger eggs, and its excretory vesicle extends much farther forward.

Bucephalopsis arcuatus was reported from *Sarda sarda* at Woods Hole by Linton (1900) and from *Scomberomorus regalis* at Beaufort, North Carolina. The latter specimen might not be *B. arcuatus*, judging from its large size and relatively short cirrus sac.

Prosorhynchus atlanticus, n. sp.

(Figures 18, 19)

Synonyms. *Gasterostomum* sp. Linton, 1910, p. 79, from *Mycteroperca bonaci*

Gasterostomum sp. Linton, 1910, p. 80, from *Mycteroperca venenosa*

Hosts. *Mycteroperca bonaci* (Poey), type host

M. microlepis (Goode & Bean)

M. venenosa (Linn.)

Location. Usually in the ceca; sometimes in the stomach; sometimes in the intestine

Frequency. Present in 2 of 5 *M. bonaci*; in 1 of 1 *M. microlepis*; in 1 of 5 *M. venenosa*

Diagnosis (based on about 20 specimens). Length 0.705 to 1.677; width 0.200 to 0.300. Anterior end truncate; posterior end tapering and somewhat pointed. Rhynchus large, muscular, cone-shaped; 0.172 to 0.277 long by 0.125 to 0.210 wide. Mouth slightly anterior to midbody in all specimens collected. Pharynx 0.042 to 0.059 in diameter; intestine short, saclike, extending forward. Gonads tandem or slightly diagonal, more or less to the right of midline, about at midbody level, near pharynx. Ovary pretesticular, globular, to right of pharynx. Vitelline follicles large, arranged in two separated lateral groups extending from about pharynx level halfway to anterior end of body; 11 to 16 follicles on each side. Yolk ducts uniting between testes. Uterus almost never extending anterior to ovary (slightly so in 1 of 29 specimens) and always extending posterior to genital pore. Eggs ovoid, thick-shelled, brown, 27 to 34 by 14 to 22 microns; average about 30 by 17 microns.

Testes ovoid, tandem or diagonal (usually diagonal), usually slightly separated. Cirrus sac well developed but usually not extending to posterior testis, only rarely (in young specimens) extending anterior to

posterior testis, with tubular, coiled seminal vesicle. Genital pore ventral, a short distance anterior to posterior end of body. Excretory pore terminal, vesicle reaching to level of pharynx.

The name *atlanticus* is for the locality.

Comparisons. *Prosorhynchus atlanticus* is most similar to *P. pacificus* Manter, 1940, collected from related hosts in the tropical Pacific. It differs in larger egg size (27 to 34 by 14 to 22 microns as compared with 24 to 27 by 12 to 17 microns), and the eggshell definitely tends to be thicker and darker in color. These differences might be considered sub-specific by some. As in the case of *P. pacificus*, the large size of the rhynchus, the separated vitelline follicles, and the postovarian uterus distinguish *P. atlanticus* from other species.

***Prosorhynchus promicropsi*, n. sp.**

(Figures 20-22)

Host. *Promicrops itaiara* (Lichtenstein)

Location. Ceca and intestine

Frequency. Present in all of 3 hosts examined

Diagnosis (based on 17 specimens). Body elongate, cylindrical, 1.498 to 1.957 by 0.276 to 0.390; anterior end truncate, posterior end more tapering; most of body about equally wide. Rhynchus cone-shaped, well developed, 0.157 to 0.277 in width by 0.195 to 0.292 in length. Mouth very slightly anterior to midbody; pharynx 0.053 to 0.073 in diameter; esophagus longer than pharynx; intestine elongate, saclike, extending forward. In 13 of 17 specimens, the intestine extended anteriorly beyond the vitellaria, and it may reach beyond the posterior border of the rhynchus (fig. 21).

Gonads more or less tandem or diagonal, in midbody region. Ovary slightly to the right or to the left, pretesticular, anterior to pharynx, opposite (and dorsal to) esophagus or intestine, usually overlapping anterior testis dorsally. Mehlis' gland postovarian, dorsal to anterior testis. Vitelline follicles forming two separated, rather compact groups clustered in the pharynx-ovary-testis region; sometimes entirely posterior to ovary, sometimes entirely between the testes, never more than a few preovarian follicles. Uterus entirely postovarian, often entirely posterior to anterior testis, always extending to extreme posterior tip of body. Eggs 25 to 31 by 17 to 20 microns but more uniform in size within any one specimen.

Testes tandem or diagonal, separated by uterus and usually by a few vitelline follicles; anterior testis close to or overlapping ovary. Cirrus sac relatively short and broad, about 1/3 to 1/4 body length (in contracted specimens it may be 1/2 body length), 0.450 to 0.545 by 0.112 to 0.142,

not reaching posterior testis; seminal vesicle elongate, almost always $1/2$ length of cirrus sac or more; pars prostatica and seminal vesicle overlapping for $1/2$ or more of their lengths, connected by a somewhat coiled tube (fig. 22). Genital atrium not appreciably wider than cirrus sac; dorsal genital lobe somewhat larger than ventral, atrial tube short; genital pore some distance (0.144 to 0.262) anterior to posterior end of body.

Excretory vesicle reaching to anterior testis. Nervous system sometimes conspicuous; transverse fibers extend across dorsal posterior portion of rhynchus; longitudinal nerves far lateral.

The name *promicropsi* is for the host.

Comparisons. This species differs from most others in the genus in the following combination of characters: far anterior extent of intestine, extent of the separated, bunched vitellaria, and the postovarian uterus. It seems to be most similar to *P. gonoderus* Manter, 1940, from which it differs in more posterior mouth and gonads and in that the intestine almost always extends anterior to the vitellaria. It differs from *P. costai* Travassos, Artigas, and Pereira, 1928, in much smaller eggs and in more posterior extent of uterus. It differs from *P. pacificus* Manter, 1940 and *P. atlanticus* in anterior extent of the intestine and in lesser longitudinal extent of the vitellaria. Also, eggs of *P. promicropsi* tend to be relatively wider, and the cirrus sac never reaches the posterior testis, whereas it may or may not in *P. atlanticus* and *P. pacificus*. The *Prosorhynchus* species of groupers are all similar but can be distinguished from one another by slight differences.

Prosorhynchus ozakii Manter, 1934

Host. *Epinephelus niveatus* (Cuv. & Val.)

Location. Intestine

Frequency. Present in 1 of 3 hosts examined

This species was reported by Manter (1934, p. 267) from a depth of 90 fathoms. It is also reported (Manter, 1940, p. 339) from related hosts along the Pacific coast of Mexico.

Dollfustrema gravidum, n. sp.

(Figures 23-26)

Synonym. *Gasterostomum* sp. Linton, 1910, p. 79, from "*Lycodon-tis moringa*"

Host. *Gymnothorax moringa* (Cuv.)

Location. Intestine

Frequency. 5 specimens in 1 of 2 hosts examined

Diagnosis (based on 4 specimens). Body plump, ovoid, 0.840 to 1.512 by 0.525 to 0.675; widest near anterior end; anterior end bluntly rounded or truncate, posterior end more pointed. Rhynchus weakly developed and flattened but with short longitudinal muscles alternating with glandular (?) regions. Anterior end of body at posterior edge of rhynchus provided with a triple-row ring of large spines (fig. 24). These cephalic spines are numerous, arranged in three alternating rows, much larger than body spines. Mouth well posterior to midbody; pharynx ovoid, 0.119 to 0.153 long by 0.085 to 0.102 wide; intestine very large, extending forward to base of rhynchus, thus being more than $1/2$ body length. The intestine often has one or more swellings and may be bent back at its anterior end as if too long for the body.

Gonads in midbody region, tandem or in triangular arrangement (probably the normal condition). Ovary either between testes (fig. 23) or to the left beside anterior testis and directly anterior to posterior testis. Ovary ovoid to subtriangular in shape; Mehlis' gland at right posterior edge of ovary. Vitelline follicles large, irregular in shape, usually so compactly close together as to appear fused, sometimes widely scattered, in two separate groups from level of ovary about halfway to anterior end. Uterus filling entire body except for a few small areas near pharynx, intestine, or cirrus sac, and a narrow strip across the body at base of rhynchus; covering most organs. Eggs (fig. 25) large, ovoid but tapering somewhat toward anterior end; 24 to 26 by 16 to 18 microns.

Testes globular or irregular in shape, somewhat larger than ovary; anterior testis usually to the right, dorsal to intestine; posterior testis about at pharynx level. Cirrus sac (fig. 26) relatively small; not reaching posterior testis; 0.207 to 0.277 by 0.080 to 0.090; seminal vesicle about $1/2$ length of sac, curving backward before entering the looped, colorless connecting tube; genital atrium moderately small; genital pore near posterior end of body. Excretory system not seen.

The name *gravidum* refers to the large number of eggs filling the body.

Comparisons. Only one other species, *D. vaneyi* (Shen, 1930), is known in the genus. *Dollfustrema gravidum* differs in the large size of the intestine and the poor development of the rhynchus. The egg size of *D. vaneyi* is not known.

Recently the author (Manter, 1940) was inclined to consider *Dollfustrema* Eckmann, 1924 a synonym of *Mordvilkovia* Pigulewsky, 1931. Such a conclusion is probably correct but assumes the presence of cephalic spines in *Mordvilkovia*. Until it is more certain that these are present, the description of Pigulewsky probably should be accepted and the genus characterized by "cuticular folds" on the rhynchus.

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EXPLANATION OF FIGURES

All figures were drawn with the aid of a camera lucida. The projected scale has the value indicated in each figure. The following abbreviations are used:

<i>cd</i> , connecting duct between seminal vesicle and pars prostatica; possibly an empty portion of the seminal vesicle	<i>gp</i> , genital pore
<i>cs</i> , cirrus sac	<i>i</i> , intestine
<i>ex</i> , excretory vesicle	<i>m</i> , mouth
<i>ga</i> , genital atrium	<i>pp</i> , pars prostatica
<i>gl</i> , genital lobe	<i>rh</i> , rhynchus
<i>glc</i> , glandular cells	<i>sv</i> , seminal vesicle
	<i>ut</i> , uterus
	<i>yd</i> , yolk duct

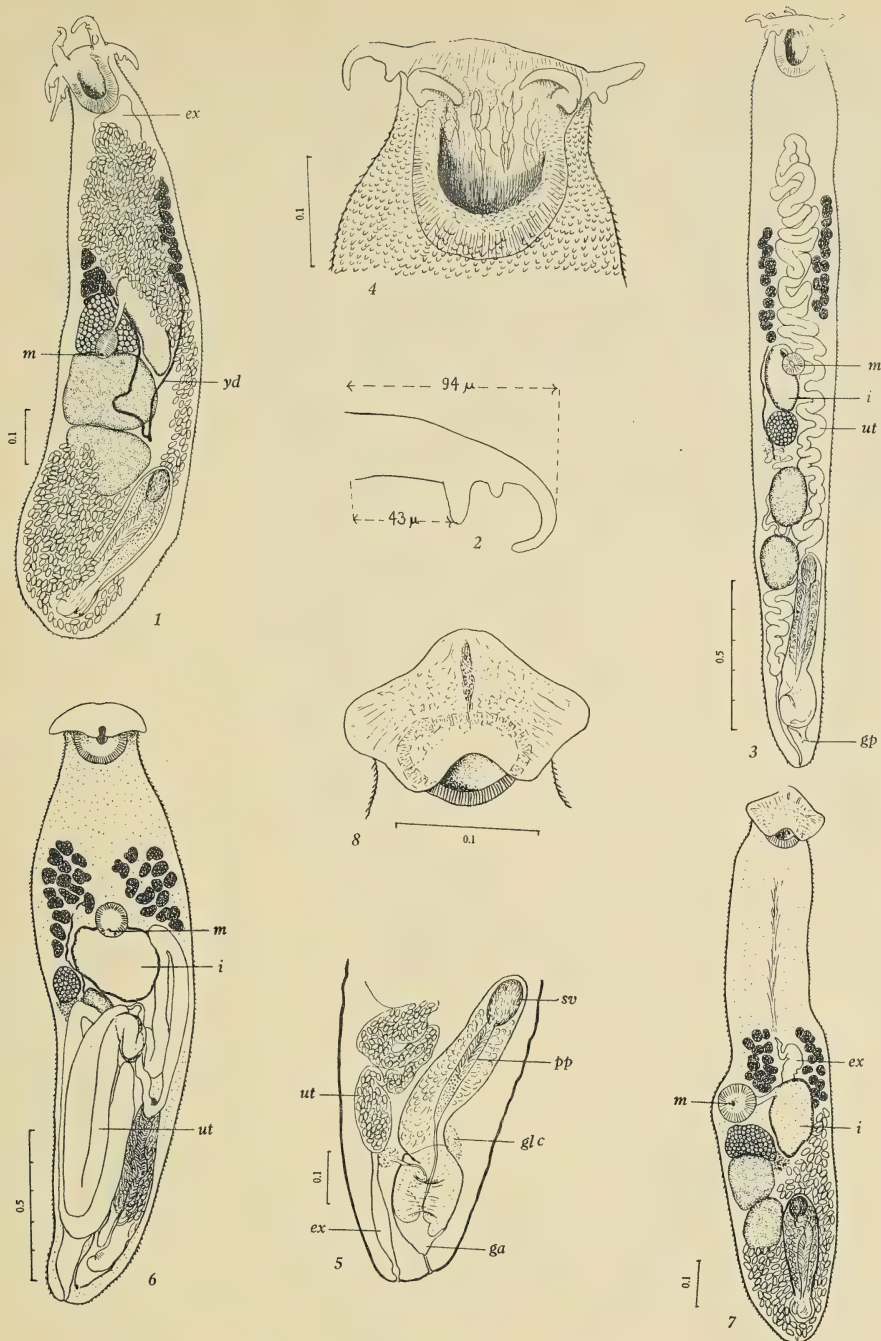


Fig. 1. *Bucephalus priacanthi* from *Priacanthus arenatus*. Ventral view.
 Fig. 2. *B. priacanthi*. Enlarged view of tentacle.
 Fig. 3. *Bucephalus scorpaenae* from *Scorpaena plumieri*. Ventral view.
 Fig. 4. *B. scorpaenae*. Enlarged view of anterior end.
 Fig. 5. *B. scorpaenae*. Enlarged view of posterior end.
 Fig. 6. *Rhipidocotyle nagaty* from *Euthynnus alletteratus*. Ventral view.
 Fig. 7. *Rhipidocotyle barracudae* from *Sphyrna barracuda*. Ventral view.
 Fig. 8. *R. barracudae*. Enlarged view of anterior end.

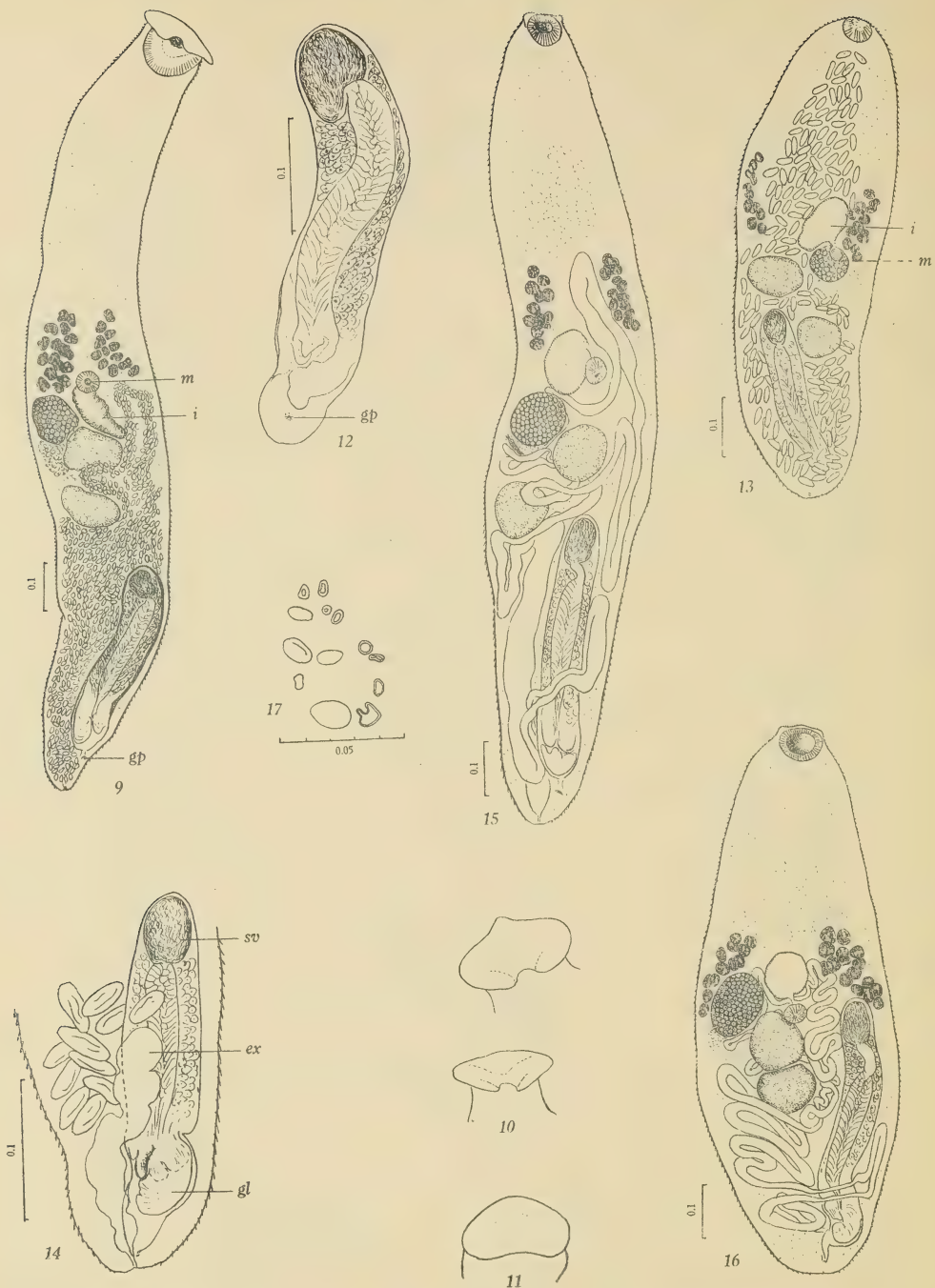


Fig. 9. *Rhipidocotyle adbaculum* from *Scomberomorus regalis*. Ventral view.
 Fig. 10. *R. adbaculum*. Enlarged view of anterior end, showing cephalic disc.
 Fig. 11. *R. baculum*. Enlarged view of cephalic disc.
 Fig. 12. *R. adbaculum*. Enlarged view of cirrus sac.
 Fig. 13. *Bucephalopsis longoviferus* from *Sphyraena barracuda*. Dorsal view.
 Fig. 14. *B. longoviferus*. Enlarged view of posterior end.
 Fig. 15. *Bucephalopsis arcuatus* from *Sphyraena barracuda*. Ventral view.
 Fig. 16. *B. arcuatus*. Ventral view.
 Fig. 17. *B. arcuatus*. Enlarged view of abnormal eggs.

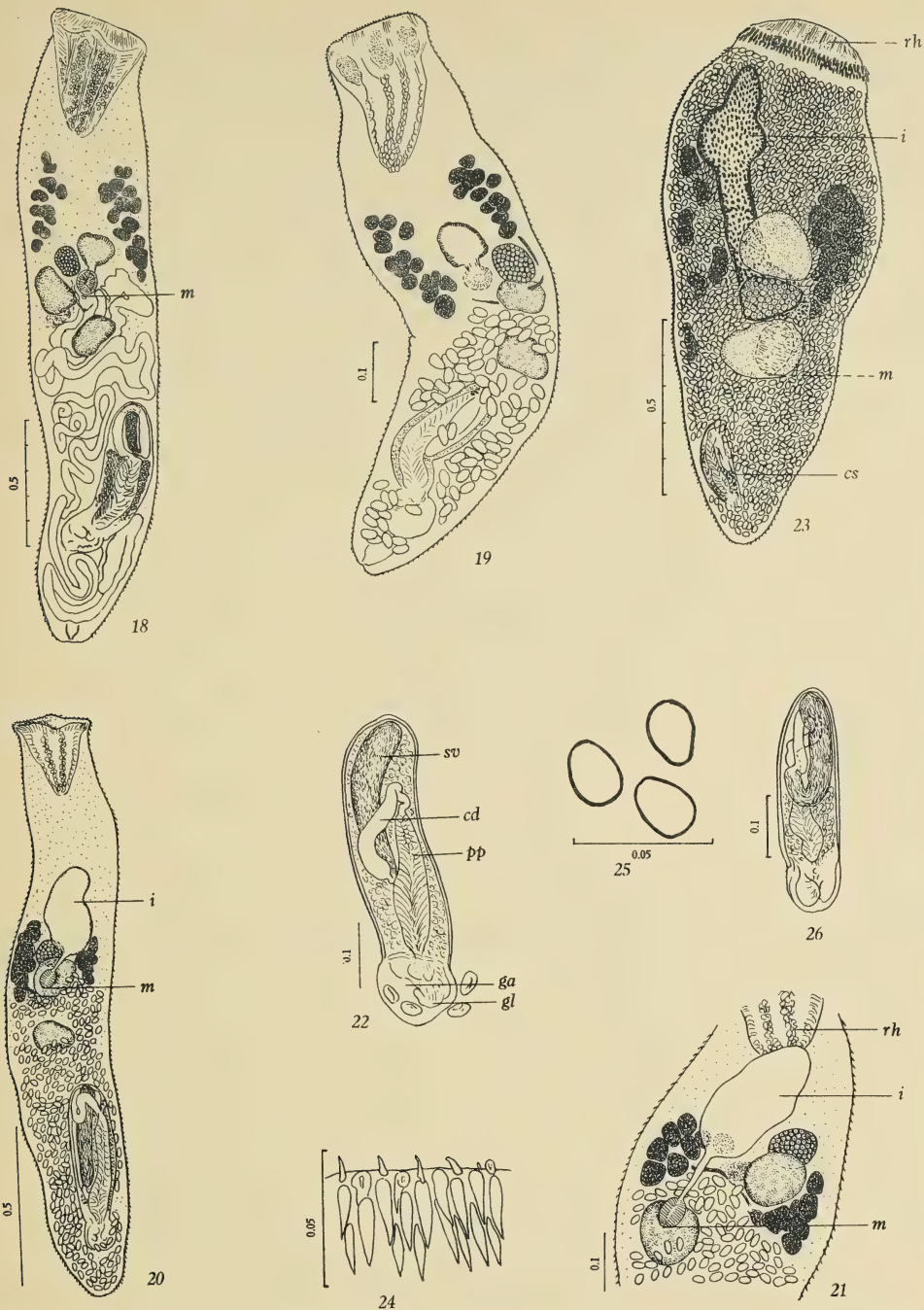


Fig. 18. *Prosorhynchus atlanticus* from *Mycteroperca microlepis*. Ventral view.
 Fig. 19. *P. atlanticus* from *Mycteroperca bonaci*. Dorsal view.
 Fig. 20. *Prosorhynchus promicropsi* from *Promicrops itaiara*. Ventral view.
 Fig. 21. *P. promicropsi*. Enlarged ventral view of anterior portion of the body.
 Fig. 22. *P. promicropsi*. Enlarged view of cirrus sac.
 Fig. 23. *Dollfustrema gravidum* from *Gymnothorax moringa*. Dorsal view.
 Fig. 24. *D. gravidum*. Enlarged portion of body showing cephalic spines.
 Fig. 25. *D. gravidum*. Eggs.
 Fig. 26. *D. gravidum*. Enlarged view of cirrus sac.

II

SWARMING OF THE ATLANTIC PALOLO WORM,
LEODICE FUCATA (EHLERS)

By LEONARD B. CLARK

Union College

and WALTER N. HESS

Hamilton College

With eight text figures

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SWARMING OF THE ATLANTIC PALOLO WORM, LEODICE FUCATA (EHLERS)¹

INTRODUCTION

Many investigators claim that various organisms show reproductive activity coinciding with some phase of the lunar cycle. The first brought to the attention of zoologists was the "palolo" worm from the Samoan Islands (Stair, 1847). As a result of numerous publications (Stair, 1847; Friedlaender, 1898; Collin, 1897; Woodworth, 1907), the Samoan name has come into common use to designate a group of worms of somewhat diverse systematic position but of similar reproductive habits. In these forms the gonads are usually limited to certain segments which at reproduction break from the rest of the body and swim to the surface, where they discharge their products. In all cases typical mass activity occurs which has led investigators to conclude that the reproduction period is concentrated into one, two, or three days, during which the sexual ends appear at the surface of the ocean in immense numbers. Such aggregations have been designated swarms. Swarming apparently is closely correlated with certain lunar phases during certain months of the year. However, there is no uniformity as to the phases of the moon or months involved, as is shown in table 1. Other worms show lunar periodicity in swarming, for example *Nereis limbata* of the Atlantic coast, reproducing most abundantly on the full moon in June, July, and August (Lillie and Just, 1913); *Platynereis dumerilii* of Europe, on the first and last quarter moons in May, June, July, August, and September (Hempelmann, 1911; Fage and Legendre, 1923); *Odontosyllis enopla* from Bermuda (Galloway and Welch, 1911); and a Bahaman species of *Odontosyllis*, the reproduction of which is closely associated with the last quarter moon in January, April, May, July, October, and December (Crawshay, 1935).

The only known occurrence of a palolo in the western hemisphere is that first reported by Mayer in 1900. At that time he erroneously believed it a new species, which he named *Staurocephalus gregaricus*, and thought that the complete worm participated in swarming. Friedlaender (1901) and Verrill (1900) both questioned this conclusion. In 1902, Mayer showed that the worm had been described as *Eunice fucata* by Ehlers (1887), from material collected by dredging in the West Indies,

¹The authors wish to express their thanks to the Carnegie Institution of Washington for the opportunity to work at the Tortugas Laboratory, and especially to Professor David H. Tennent, the Executive Officer of the Laboratory, for thoughtful assistance. The authors express their appreciation to Mr. C. A. Park, Bureau of Lighthouses, U. S. Coast Guard, for help in securing meteorological data. The assistance of Mr. Z. Peter Grabicki is gratefully acknowledged.

and he gave a correct interpretation of swarming. During the next few years his further observations resulted in numerous important papers (1908, 1912, 1914, 1916), of which the most significant were perhaps those of 1908 and 1912. He concluded that swarming occurs within 3 days of the day of the last quarter moon between June 29 and July 28, except when the last quarter occurs late in July, in which case the worms may swarm at the previous first quarter.

Treadwell (1914, 1917, 1921) changed the name of the worm to *Leodice fucata* and added observations on natural history, distribution, and swarming. Except for Longley (1924), who listed fishes feeding on palolo, Bullington (1930), who studied the spiral movements of palolo

Table 1. Showing relation of moon's phases to reproduction in worms commonly called "palolo"

Species	Month of swarming	Moon's phase	Reference
<i>Eunice viridis</i>	Oct. or Nov.	Last quarter	Woodworth, 1903
<i>Lysidice oele</i>	Mar. or Apr.	Full moon	Horst, 1905
<i>Ceratocephale osawai</i> ..		Full or new moon	Izuka, 1903
<i>Leodice fucata</i>	July	First or last quarter	Mayer, 1908
<i>Lysidice falax</i>	Oct. or Nov.	Last quarter	Woodworth, 1903

embryos, and Hess (1931), who observed the light reactions of the adults, other references to the Atlantic palolo are records of dates of swarming only.

Swarming has been reported from Andros Island in the Bahamas and at Montego Bay, Jamaica (Treadwell, 1921), but it occurs commonly only at the Dry Tortugas Islands. A summary of the dates of swarming to 1936 with dates of the moon's phases is given in table 2. The date of the maximum swarm is italicized when known. Figure 1 shows the distribution of swarming as related to lunar periodicity. The solid line indicates the amount of darkness, that is, the time when neither the moon nor the sun is above the horizon during the lunar cycle. It will be seen that, in general, swarming occurred about the time of the third quarter, although some swarms occurred at the first quarter and one is reported at the time of the full moon.

Mayer (1908, 1909) claimed that worms were inhibited from swarming if the rocks containing them were darkened from moonlight for 2, 5, 14, or 30 days before the date of the swarm. Although Treadwell (1909) showed that withdrawal of light for one night is not sufficient to inhibit swarming, there seems little doubt that longer periods of shading from moonlight are effective in preventing swarming.

The data presented in table 2 and figure 1, collected by many different observers over a series of years, supported by the shading experiments of Mayer and Treadwell, and considered in connection with reproductive activities in other forms, seem to give conclusive evi-

Table 2. *Dates of swarming of Leodice fucata at the Dry Tortugas Islands, Florida*

(Date of maximum swarm italicized where known.
F.Q., first quarter; L.Q., last quarter.)

Year	Swarming dates	Moon's phase and date	Reference
1898.....	July 9, 10	L.Q., July 10	Mayer, 1908
1899.....	July 1, 2	L.Q., June 29	Same
1900.....	July 19 (others unknown)	L.Q., July 18	Same
1902.....	July 24, 25, 26	L.Q., July 27	Same
1903.....	July 17 (others unknown)	L.Q., July 17	Same
1905.....	July 9, 10	F.Q., July 9	Same
	July 21, 22, 23, 24	L.Q., July 24	Same
1906.....	July 11, 12, 13	L.Q., July 13	Same
1907.....	July 2, 3	L.Q., July 2	Same
1908.....	July 10	F.Q., July 6	Same
	July 19	L.Q., July 19	Same
1909.....	July 6, 7	L.Q., July 9	Treadwell, 1909
1910.....	July 29, 30	L.Q., June 30	Mayer, 1914
1911.....	July 16, 17	L.Q., July 18	Same
1912.....	July 6, 7	L.Q., July 7	Same
1914.....	July 11	L.Q., July 14	Same
1915.....	July 1	L.Q., July 3	Treadwell, 1915
1916.....	July 14	Full, July 14	Mayer, 1916
	July 20	L.Q., July 20	Same
1922.....	July 16	L.Q., July 17	Potts, 1922
1923.....	July 7	L.Q., July 5	Longley, 1924
1924.....	July 22	L.Q., July 23	Grave, 1924
1925.....	July 10	L.Q., July 12	Grave, 1925
1929.....	June 28, 29, 30, July 1, 2, 3, 4	L.Q., June 30	Grave and Burkenroad, 1929
	July 17, 18	F.Q., July 13	Same
1930.....	July 16	L.Q., July 18	Bullington, 1930
1931.....	July 4, 8, 9	L.Q., July 7	Hess, personal communication
1936.....	July 10, 11, 12, 13	L.Q., July 11	Plough, personal communication

dence that lunar periodicity controls swarming in *Leodice fucata*. Early in the present investigation, it became apparent that factors other

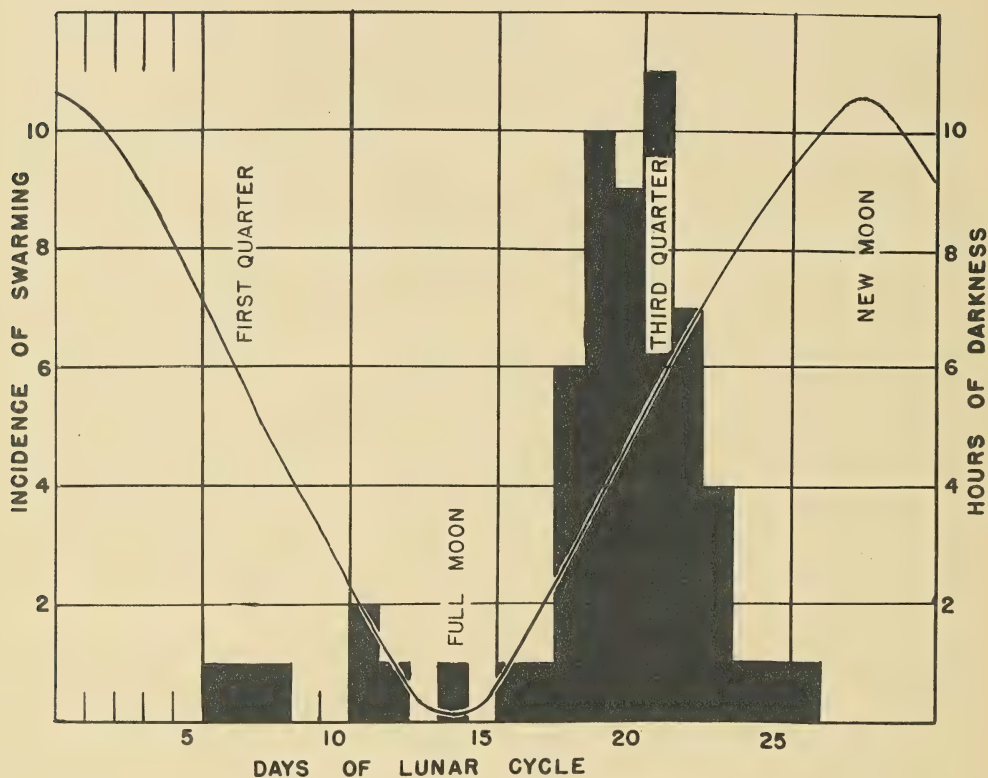


Fig. 1. Swarming in the Atlantic palolo as related to the lunar cycle. Records of the major swarm over Bird Key Reef in 1937, 1938, and 1939 are included with all records from 1898 to 1936. *Hours of darkness*, time during which both sun and moon are below the horizon.

than lunar periodicity were involved in swarming. It will be shown in this paper that the velocity of the wind and the sexual maturity of the worms are also important factors. It seemed advisable to follow the course of events during swarming to ascertain its onset, time relations during the swarm, and the influence of sunlight on the cessation of swarming. The present paper proposes to deal with these problems primarily from observation in the field.

LIFE HISTORY OF THE ATLANTIC PALOLO
AND DESCRIPTION OF ITS SWARMING

Leodice fucata is widely distributed in the West Indies region, being reported from the Dry Tortugas Islands, Porto Rico, Cape Florida, Jamaica, Tobago Bay, and the Bahamas (Treadwell, 1921). The worms live in crevices and burrows in dead coral or in limestone beach rock from the lower levels of the intertidal zone to about 150 fathoms. They can excavate their own burrows, but usually incorporate into them cavities and tunnels made by other organisms, such as burrowing mollusks and serpulid worms. Although the rock may be honeycombed and yield as many as 20 worms per cubic foot, the burrows do not seem to communicate with each other. The worms are negative to all except very weak intensities of light, and remain in their burrows during the day. At night the anterior end is protruded into the water. Examination of the intestinal contents indicates that the food consists largely of vegetable matter secured by the worm within a few inches of the mouth of the burrow.

During the night of swarming the worm backs out of its burrow and the caudal sexual portion, or epitoke, begins a series of convulsive twisting movements, usually but not always counterclockwise, during which the epitoke is torn from the anterior, or atokal, portion, which crawls back into the burrow. The epitoke swims to and at the surface in a series of graceful spiral movements. The epitoke, usually about half the total length of the worm, may vary from two-fifths to three-fifths of the total. Each of its segments except the anterior two or three and the posterior thirty or forty has a pair of much enlarged gonads, which constrict the intestine and blood vessels and distend the coelomic cavity. The posterior thirty to forty segments, from which gonads are absent, are different in color and much smaller. The epitoke swims with this nonsexual portion foremost, and the spiral movement is initiated there. However, as pointed out by Mayer (1908), any part of the epitoke large enough to swim will continue to swim in spirals with the morphological posterior foremost.

According to Mayer (1908), swarming begins in the early morning between 3:00 and 4:00 a.m. and the numbers of swimming individuals increase rapidly until dawn, when the surface of the ocean is covered. With the rising of the sun the epitokes yield up their reproductive products by the almost instantaneous rupturing of the lateral body walls. Bullington (1930) noted that they swarmed from early dawn until the sun was about half an hour high, at which time all had ruptured. The empty epitokes may swim for a short period unless eaten by fish (Longley, 1924, lists fishes which eat palolo), but they soon sink to the bottom and die, although in the laboratory exhausted epitokes have remained alive for as long as 8 days.

After being discharged the eggs float and may appear in such immense numbers that they cover the ocean for acres. Grave (1924, 1925) noted that long windrows of eggs occurred, several yards in width and several feet in depth, and that the water contained thousands of eggs per bucketful.

The eggs are immediately fertilized and proceed through their cleavage stages, so that by 10 o'clock in the forenoon they may be in late segmentation. By late evening or the next morning they are ciliated larvae, swimming with the spiral motion described by Bullington (1930). The larvae are positive to light and negative to gravity for 3 days, after which they sink to the bottom.

Mayer (1908) pointed out the difficulty of keeping the Atlantic palolo in aquaria. They seem to be very sensitive to lack of circulation, to CO₂, and to impurities in the water. If small pieces of rocks containing the worms are put into aquaria, the worms die within a very few days even though a flow of water is maintained sufficient to give a complete change every 15 minutes. It was hoped that a method could be developed by which mature worms could be removed from their burrows and put into aquaria. Attempts to drive out the worms by desiccation of the rocks, by putting the rocks into warm water, and by the electric current all failed completely. The worms have the power of autotomy developed to a remarkable degree. Any nocuous stimulus sufficient to overcome their positive thigmotropism is more than sufficient to cause them to fragment. Also the epitokal end is very sensitive to light and usually starts twisting movements when exposed, so that it is broken off the atoke and may even be broken into a number of pieces. Not a single complete mature specimen was secured by any of the above methods. A measure of success was attained by breaking open the rocks with a cold chisel. It was necessary to work in dim light, as at dusk, and to expose the worm completely with one blow. If any part of the worm, especially the anterior end, remains in the burrow, it crawls in, and even gentle pulling causes it to break. Very often the weight of part of the worm is sufficient to cause autotomy. With experience it was found possible to remove unbroken from their burrows about 5 per cent of the mature worms. They did not live free in aquaria even in the darkroom. Various attempts were made to keep them in glass tubes covered with rubber tubing, but without success. The worms readily entered the tubes and remained in them during the daytime, but left them at night and did not find their way back. At sunrise they were so strongly stimulated by light that they fragmented.

The sexual ends, if broken out of rocks, behave much like those in the process of swarming if the light intensity is more than half a foot-candle. They twist, break away, and swim at the surface much in the manner of normal swarming. Treadwell (1914) believed this was due to the contact stimulus of open water, to which they are not exposed before swarming; we have found, however, that worms broken out of rocks

in the dark do not react, but that once the reaction has been inaugurated, darkness does not inhibit it. Treadwell pointed out that this reaction is not shown by immature individuals but becomes more marked as the animals approach maturity. We have found that the posterior end likewise becomes more sensitive to light as the animal approaches maturity.

Owing to the difficulties mentioned, it was impossible to keep worms for more than a few days in the laboratory.

CHANGES ASSOCIATED WITH SEXUAL MATURITY

As the season for the swarming of the palolo worm approaches, certain important changes occur in the animal in preparation for the release of the epitoke. The maturing sex cells cause the epitoke of the male to assume a deep pink and that of the female a greenish-gray color, making the epitoke easily distinguishable from the atoke. The enlargement of the gonads, which greatly distend the coelomic cavities, is accompanied by a thinning of both muscle layers of the body wall (fig. 2). The two or three anterior segments of the epitoke become differentiated, forming a junction for its release. Since the segments of the junction do not form germ cells, or at most only a few, and since they are a part of the epitoke and hence have thin walls, the worm becomes constricted in this region. Owing to poor circulation through the junction, the dorsal blood vessel and certain of the parietal blood vessels usually become distended with blood, and this change, together with those mentioned above, makes a junction which is easily ruptured. One of the striking phenomena accompanying reproduction is the great increase in activity of the posterior end and the breaking of the epitoke from the atoke, as described above. Muscular contractions resulting in spiral or twisting movements are initiated at the posterior end even before the separation of the epitoke takes place.

A study of the oxygen consumption of mature and immature individuals was made to secure information regarding the physiological changes occurring in different regions of the body.

Complete worms were broken out of rocks and cut at four levels, giving five pieces designated by the numbers 1 to 5. These pieces consisted of: (1) the anterior half of the atoke; (2) the posterior half of the atoke; (3) the anterior half of the sexual portion of the epitoke; (4) the posterior half of the sexual portion of the epitoke; and (5) the nonsexual posterior portion of the epitoke. Each piece was put into a calibrated glass-stoppered bottle of approximately 60 cc. capacity, filled with filtered sea water. A sample of the water was titrated to determine the oxygen tension and then all experimental bottles and a control were put into a closed metal container filled with sea water and suspended in the ocean 2 feet below the surface. The du-

ration of the experiment varied, but in all cases attempts were made to regulate the time so that not more than three-fifths of the available oxygen was used. Oxygen tension was determined by a modified micro Winkler method, using 0.00415 N thiosulphate. At the close of the experiment the surface water was removed from the pieces of worms by laying them on filter paper. They were then weighed and put individually into finger bowls with sea water. If all pieces remained in good condition, they were used again the next day.

A control was run with the experimental bottles, and the decrease in oxygen per cubic centimeter due to bacteria and other microorganisms as found in the control was deducted from the total oxygen decrease found in the experimental bottles. The results are given in table 3 in oxygen

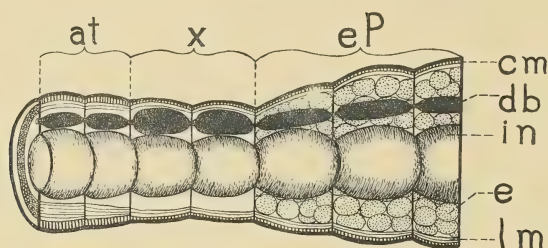


Fig. 2. Semidiagrammatic drawing of a longitudinal section of the junction of the atoke and epitoke of a sexually mature female worm. *at*, atoke; *cm*, circular muscles; *db*, dorsal blood vessel; *e*, eggs; *ep*, epitoke; *in*, intestine; *lm*, longitudinal muscles; *x*, differentiated segments at junction of atoke and epitoke.

consumption per gram per minute times 10^3 . Immature worms are indicated by asterisks in the column showing the sex.

The peculiarly intractable nature of the organism amplifies the difficulties and increases the sources of error normally present in determinations of oxygen consumption. During removal from the rocks and during the manipulation necessary to carry on the experiment, the animal is apt to go to pieces, and the epitokal sections may begin to swim vigorously and to shed eggs. The results presented are the only ones obtained from some dozens of attempts. The individual results are therefore not considered accurate, but certain general conclusions are indicated.

Table 3 shows that in two of the three immature females tested the anterior end had the highest rate of oxygen consumption, while in all except one of the mature animals the posterior, nonsexual portion of the epitoke was the most active. This suggests that metabolic dominance shifts from the anterior to the posterior end of the animal with sexual maturity. Confirmation of the idea of a progressive shift was sought in a comparison of the ratios of the rate of oxygen consumption of the anterior end to that of the posterior in those animals tested before July 2 (table 3, experiments 1, 2, 4, and 5) and those tested after July 12 (experiments 8, 9, 10, and 11). In the former group the

average ratio of the rate of oxygen metabolism of the head end is 1:2.4, while that of the latter is 1:2.9, showing an increase in rate of the posterior end as compared with the anterior of almost 25 per cent.

When rates of oxygen consumption of the other pieces are compared with one another and with those of the anterior and posterior pieces, the results are quite unreliable. Pieces 2, 3, and 4 have two cut surfaces each, and Parker (1929) has shown that the area of injury increases metabolism. Pieces 3 and 4 contain sex products, and Treadwell (1914) found that eggs more than double their rate of metabolism in the 5 days immediately preceding swarming.

It is believed, however, that a comparison between the rate of metabolism of the anterior atokal portion (piece 1) and that of the posterior epitokal portion (piece 5) is significant. Each piece has only one cut surface and both pieces are free of eggs. Therefore it may be concluded that the respiration experiments do show a change in the region of greatest metabolism from the anterior end in immature animals to the posterior end in mature forms. If this coincides with a change in physiological gradient and dominance, it follows that maturing of the sexual product in preparation for swarming is accompanied by decrease of dominance of the anterior end, with a concomitant increase at the posterior end. This may be the factor, or one of the factors, involved in what the authors have called maturity, and may not be accompanied by any gross morphological or histological change.

COMPARISON OF SWARMING OVER WEST LOGGERHEAD REEF AND BIRD KEY REEF IN 1937, 1938, AND 1939

All previous reports of swarming except those of Grave and Burkenroad (1929) were based upon observations of epitokes in the water in the early morning. Consequently it is possible that small swarms occurred without being noticed. Grave and Burkenroad, by observation of epitokes supplemented by towing for newly laid eggs, report swarming on 8 days in 1929. The only other record nearly as extensive is that for 1905, with swarming on 6 days, while of the remaining 22 years listed, 4 days of swarming are reported for 1 year, 3 days each for 3 years, 2 days and 1 day for 9 years each.

Since eggs fertilized the preceding night or in the morning will be in late segmentation stages by 10 o'clock in the forenoon, and eggs fertilized 24 hours or more will have developed into ciliated larvae, the finding of cleaving eggs in a morning tow shows definitely the presence of a swarm earlier in the morning. There can be no confusion between eggs laid on different days. For this reason systematic daily towings supplemented observations made at intervals during the night and at dawn. The quantity of eggs recovered would give some indica-

Table 3. *Oxygen consumption of pieces from different levels in mature and immature worms*
(A indicates the piece with the highest rate and E the lowest. F, female; M, male.)

Exp.	Date (1938)	Sex	Av. temper- ature (°C.)	Section of worm	Duration (min.)	Weight (g.)	O ₂ consump- tion (cc.)	O ₂ con- sumption per g. per min. × 10 ³	Relative rate O ₂ consumption	Ratio of rate of O ₂ consumption ant. piece to post. piece
1.....	6/24	F	29.0	1 2 3 4 5	715 725 735 750 710	0.426 0.0493 0.534 0.187 0.337	0.232 .129 .405 .735 .392	0.763 0.265 1.031 0.523 1.120	D E B C A	1:1.47
2.....	6/25	F	28.6	1 2 3 4 5	635 630 710 695 713	0.595 0.536 0.423 0.337 0.498	.156 .134 .158 .149 .439	0.413 0.399 0.526 0.633 1.230	D E C B A	1:2.98
3.....	6/26	F*	29.0	1 2 3 4 5	830 840 855 865 875	0.1365 0.1556 0.1065 0.1477 0.0527	.015 .0145 .0159 .0141 .0071	0.137 0.111 0.175 0.110 0.153	C D B E A	1:1.20
4.....	6/27	M	28.7	1 2 3 4 5	1095 1105 1115 1130 1140	0.7016 0.4348 0.3776 0.6245 0.2829	.167 .168 .190 .210 .211	0.217 0.433 0.452 0.2975 0.6730	E C B D A	1:3.01
5.....	7/2	M	29.1	1 2 3 4 5	560 570 585 595 610	0.563 0.347 0.284 0.767 0.432	.147 .043 .087 .467 .294	0.467 0.216 0.522 1.023 1.116	D E C B A	1:2.39

* Immature.

(Continued on following page)

Table 3 - Continued

Exp.	Date (1938)	Sex	Average temperature (°C.)	Section of worm	Duration (min.)	Weight (g.)	O ₂ consumption (cc.)	O ₂ consumption per g. per min. × 10 ³	Relative rate O ₂ consumption	Ratio of rate of O ₂ consumption ant. piece to post. piece
6.....	7/10	M*	31.5	1	190	1.5646	.258	0.969	A	1:0.47
				2	200	0.1263	.0197	0.742	B	
				3	210	0.1156	.007	0.269	D	
				4	230	1.5281	.082	0.232	E	
				5	240	0.0541	.005	0.4075	C	
7.....	7/11	M*	28.7	1	935	0.1632	.109	0.712	A	1:0.59
				2	945	0.0704	.014	0.216	E	
				3	980	0.0414	.015	0.377	C	
				4	970	0.0789	.023	0.299	D	
				5	980	0.0562	.023	0.420	E	
8.....	7/12	M	29.0	1	720	0.217	.0417	0.267	D	1:3.54
				2	735	0.436	.103	0.321	C	
				3	745	0.172	.015	0.117	E	
				4	760	0.242	.115	0.623	B	
				5	770	0.129	.094	0.945	A	
9.....	7/13	M	28.3	1	600	0.327	.083	0.421	D	1:1.89
				2	615	0.551	.177	0.522	C	
				3	630	0.321	.147	0.726	B	
				4	645	0.824	.033	0.0623	E	
				5	660	0.077	.043	0.794	A	
10.....	7/14	F	28.3	1	525	0.1565	.011	0.124	E	1:4.69
				2	540	0.1605	.049	0.567	B	
				3	550	0.1742	.027	0.216	D	
				4	565	0.1356	.042	0.550	C	
				5	575	0.1031	.035	0.582	A	
11.....	7/14	F	28.3	1	590	0.0725	.015	0.341	C	1:1.54
				2	600	0.1855	.016	0.146	E	
				3	615	0.2372	.095	0.852	A	
				4	625	0.6334	.127	0.321	D	
				5	640	0.0628	0.021	0.528	B	

* Immature

tion of the intensity of the swarm. A tow net of no. 12 silk bolting cloth was used and tows were made for 10-minute periods at the surface. Variation in the roughness of the water, the force and direction of the tide, and speed of towing, as well as clogging of the net by palolo eggs and other plankton, make quantitative counts of eggs unreliable. Therefore we grouped our positive findings into seven classes: rare, 1 or 2 eggs only in a 10-minute tow; very few, up to 10 eggs; few, from 10 to 50 eggs; fairly numerous, 50 to 100 eggs; numerous, 100 to 1000 eggs; abundant, over 1000 eggs; and very abundant, thousands of eggs clogging the net and occurring only during a maximum swarm.

Tows were made in the morning, usually before 9:30. To reduce the possibility of obtaining erroneous data as a result of the net's passing through a region with a localized concentration of eggs, such as a location where a worm had recently shed, two tows were customarily made, kept separate, and compared. In the few cases of wide divergence in number of eggs obtained on the same day, additional tows were made.

Two areas differing in certain physical features but in both of which palolo is found in abundance were subjected to intensive study. It was thought that a comparison of the incidence and time of swarming over the two areas would give some indication of those factors other than moonlight influencing swarming.

One area was West Loggerhead Reef (fig. 3), lying parallel to and northwest of Loggerhead Key. It is covered with shallow water, 1 to 3 meters deep at mean low tide, and has a gently sloping bottom, so that the 6-meter depth line lies about 0.5 kilometer offshore. The reef is well protected from south and east winds, but exposed to those from other directions.

The other area studied was that lying to the southeast of Bird Key Reef, which lies about 6.5 kilometers from West Loggerhead Reef. The water on the west side of the reef is shallow with sandy bottom and is destitute of palolo worms. On the east side worms occur in abundance in old coral rock. The bottom slopes rapidly, the 6-meter line being only about 0.1 kilometer from the reef. The water is freely exposed to wind from the south and east but well protected on the north and west.

The two areas under observation were similar in abundance of palolo, in having a dead-coral-rock and beach-rock bottom, and in being comparatively shallow. They differed in the slope of the bottom and in exposure to wind and wave action.

The observations made during 1937, 1938, and 1939 (Clark, 1937; Clark and Hess, 1938, 1939) are given in table 4. The times when major swarms of epitokes were seen are indicated by asterisks in the table.

Reproduction in the palolo worm is not restricted to a few days around the time of the third quarter moon. Small numbers of worms may spawn sporadically during any night except those immediately preceding or following the new moon. Also, it is apparent not only that there is

a variation in minor swarming between the worms at West Loggerhead and at Bird Key reefs, but that the major swarm may and does occur at different times. In 1938 the heaviest swarm of the season occurred on July 3 over West Loggerhead, while eggs were rare on the same morning over Bird Key Reef. Conversely, the major swarm occurred almost two weeks later, on July 15, over Bird Key Reef, while very few eggs were

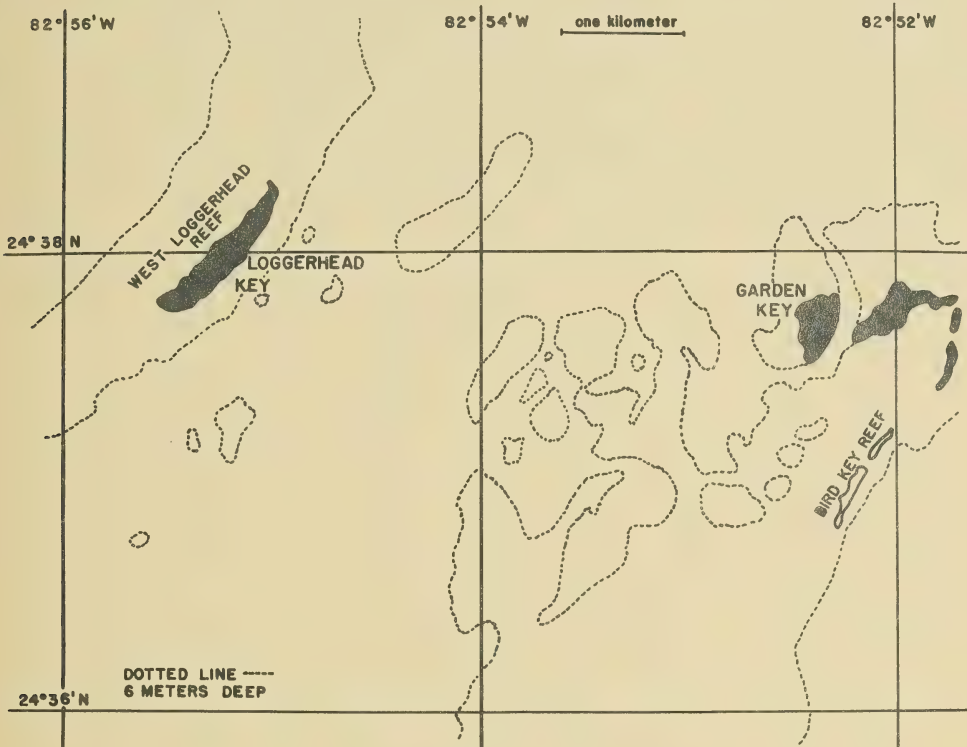


Fig. 3. Map of Dry Tortugas Islands. Swarming was studied over West Loggerhead and Bird Key reefs. West Loggerhead Reef, lying along the northwest shore of Loggerhead Key, is protected from south, southeast, and east winds. The northern side of Bird Key Reef is very shallow, with a sand bottom, and unsuitable for palolo worms. The reef is above water much of the time, and so, with Garden Key and the other islands, serves to protect the water on the east side of the reef, which is inhabited by worms, from west and north winds.

obtained from West Loggerhead. On each of these days reproduction was so intense that eggs floated in windrows over their respective reefs, and at West Loggerhead the concentration of swimming epitokes at dawn well merited Agassiz's comment that the ocean looked like "vermicelli soup." During 1937 and 1939 no major swarm took place over West Loggerhead such as was described by Mayer and seen by the authors in 1938, but such swarming did occur over Bird Key Reef on July 14, 1937 and July 6, 1939.

It was barely possible that even abundant swarms might be missed by daily observations made at dawn, as the set of the tide might sweep the swarming epitokes and released eggs beyond the area covered in towing. Consequently during 1937 and 1938 tows and observations were made at

Table 4. Recovery of newly laid eggs in tow over West Loggerhead and Bird Key Reefs at the Dry Tortugas Islands during 1937, 1938, and 1939. Dates arranged so as to make incidence of swarming on similar lunar phases easily comparable

Moon's phase	1937			1938			1939		
	Date	W. Loggerhead	Bird Key	Date	W. Loggerhead	Bird Key	Date	W. Loggerhead	Bird Key
Third quarter	July 1			June 20			June 8		
	2			21	Very few		9		
	3			22	Fairly numerous		10		
	4			23		Very few	12		
	5			24		Fairly numerous	13		
	6			25	Rare		14		
	7			26	Very few		15		
New moon...	8			27	Rare		16		
	9			28	Few	Rare	17		
	10			29	Rare	Rare	18		
	11			30	Rare	Rare	19		
	12		Few	July 1	Rare	Rare	20		
	13	Few	Numerous	2	Rare	Rare	21		
	14	Few	Very abundant*	3	Very abundant*	Rare	22	Rare	
First quarter	15	Few	Few	4	Very few	Rare	23	Few	Very few
	16	Fairly numerous		5		Few	24"	Few	Fairly numerous
	17	Few		6			25		Very few
	18	Numerous		7	Rare	Rare	26		Very few
	19			8		Rare	27	Numerous	Few
	20			9		Fairly numerous	28	Few	Very few
	21			10		Rare	29	Few	Rare
	22			11	Very few	Rare	30	Numerous	Few

*Major swarm.

"New moon on June 17.

"First quarter on June 24.

(Continued on following page)

Table 4 - Continued

Moon's phase	1937			1938			1939		
	Date	W. Log-gerhead	Bird Key	Date	W. Log-gerhead	Bird Key	Date	W. Log-gerhead	Bird Key
Full moon...	July 23			July 12			July 1	Abundant	Very few
	24			13		Rare	2	Fairly numerous	Abundant
	25			14	Rare	Very few	3		
	26			15	Very few	Very abundant*	4	Rare	Rare
	27	Numerous		16		Fairly numerous	5	Very few	Abundant
	28			17		Few	6		Very abundant*
	29			18			7		Few
	30 [#]			19			8		
	31			20			9	Few	Few
	Aug. 1	Numerous		21			10	Few	Rare
Third quarter	2			22			11	Rare	Rare
	3			23	Rare		12	Numerous	Fairly numerous
	4			24	Few		13	Fairly numerous	Few
				25			14	Numerous	Few
				26			15		Rare
				27			16		
New moon..							17		
							18	Few	
							19	Few	Fairly numerous
							20	Few	Rare
							21		
							22		

*Major swarm.

#Third quarter on July 30.

intervals during the nights when swarming would be expected to occur, and in 1939 observations and tows were taken systematically at 2-hour intervals during the nights from June 29 to July 16. As an independent check on towing and observational results, rocks containing worms were broken open and careful counts made of immature and sexually ma-

ture worms and those regenerating posterior ends.² These data are given in table 5. They show, except for the worms from Bird Key Reef in 1937 and 1938, no abrupt decrease in sexually mature forms, but rather a gradual decrease during the summer. Likewise this served as a check on the possibility that the worms had swarmed on or about June 30, 1937, near the third quarter moon of July 1, before observations were begun that year.³ As is shown in the table, no regenerating worms were found previous to July 14. In 1939 it was thought that worms might swarm after the authors left the Laboratory on July 25, and arrangements were made with Mr. Paul Conger, Assistant Executive Officer, to examine daily tows from over West Loggerhead Reef. He reports that no eggs were recovered after that date.

Therefore it may be concluded from a consideration of the data for 1937, 1938, and 1939 that:

1. Reproduction probably is not restricted to a few days, but may occur at random and sporadically over a period of almost a month (June 22 to July 20, 1939). There is a distinct diminution at the time of the new moon.
2. The heaviest swarming may not be simultaneous over a wide region. (In 1938 it occurred on July 3 over West Loggerhead and on July 15 over Bird Key Reef.)
3. Sometimes a heavy swarm of the type described by previous authors fails to materialize, but a series of what we have designated minor swarms takes place. In these minor swarms, few or no epitokes are seen swimming at dawn but eggs in cleavage stages are numerous.

The influence of light on reproduction will be treated at length in a future paper, but it must be pointed out that although the lunar cycle does not control the worms in their swarming as completely as was held by earlier observers, swarms are grouped about the time of the quarter moon (fig. 1) and recovery of newly laid eggs is rare at the time of the new moon. It should also be pointed out that in those years and over those areas in which the greatest swarms were recorded (July 14, 1937, July 15, 1938, and July 6, 1939 at Bird Key Reef; July 3, 1938 at West Loggerhead Reef), the number of worms participating in a swarm far exceeded the total of all worms appearing at other times. Thus it seems that the lunar cycle is the most potent but by no means the only factor influencing swarming.

²Regenerating worms, as counted here, include not only individuals with visible regenerating posterior segments, but also worms without visible regenerating parts such as would be found in worms which had recently swarmed.

³Dr. David H. Tennent, Executive Officer of the Tortugas Laboratory, informed one of the authors on his arrival that he had watched for swarming previous to July 2 and that none had occurred.

For three summers the authors have examined some scores of mature worms in an attempt to discover some morphological difference between the worms on the two reefs studied. In 1937 the worms from Bird Reef seemed to be in the same stage of maturity as those from West

Table 5. Number of individuals obtained from rocks
(M.M., sexually mature males; M.F., sexually mature females;
Reg., individuals with regenerating sexual ends;
Im., immature individuals)

Date	West Loggerhead Reef				Bird Key Reef			
	M.M.	M.F.	Reg.	Im.	M.M.	M.F.	Reg.	Im.
1937								
July 4.....	6	5	0	7				
July 8.....					5	2	4	0
July 9.....					1	3	12	49
July 11.....	7	12	2	11	0	0	7	11
July 16.....	5	7	5	6	0	0	14	7
Aug. 3.....	1	0	13	8	0	0	10	14
1938								
July 2.....	2	5	1	4				
July 9.....	3	1	12	46				
July 11.....					13	10	1	16
July 16.....					0	0	14	?
July 20.....	1	2	17	?	0	0	23	?
1939								
June 26.....	3	4	2	14	2	5	3	7
July 18.....	7	1	9	3				
July 20.....					0	0	7	4
July 22.....					1	2	?	?

Loggerhead, although the former yielded a major swarm and the latter did not. During 1939 specimens from Bird Key Reef collected on June 28 were compared with those collected on the same reef a year earlier. They seemed morphologically similar in development,⁴ although in 1938 they swarmed on July 15 and in 1939 on July 6.

⁴It was hoped that the development of the epitoke could be followed by planting rocks containing palolo on East Loggerhead Reef in 1937 and arranging for their collection by the staff of the lighthouse on Loggerhead Key. Preservation was inadequate.

THE COURSE OF A SWARM

During the night of July 2, 1938, the progress of a swarm was followed from its initiation until the last epitoke disappeared the next morning. The water over West Loggerhead Reef was almost a dead calm. At 9:30 p.m. freshly laid eggs were obtained in tow. Immediately free-

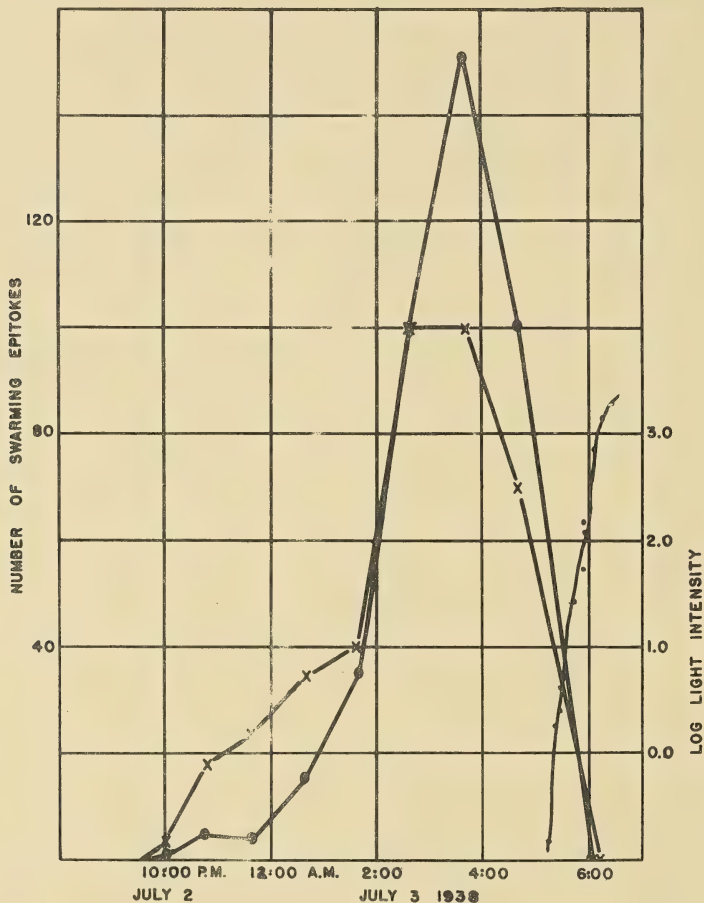


Fig. 4. Counts of free-swimming epitokes during the course of a swarm over West Loggerhead Reef on the night of July 2, 1938. x, male epitokes; o, female epitokes. *Light intensity*, incident light falling on a horizontal surface 10 feet above mean tide level.

swimming epitokes were sought, and observations were continued all night. At 9:45 and 10:15 p.m. four males and one female were seen swimming in the beam of a flashlight. During the night, counts were made of the numbers of each sex seen. The results are given in figure 4. It will be noted that in the early part of the night males were numerous, but after 3:00 a.m. females were in excess. As pointed out by Mayer (1908), the female epitokes are more delicate and fragile and

shed their sex products more readily than the males. If the ratio of the number of the two sexes leaving their burrows remained constant during the course of the swarm, it would be expected that the proportion of male epitokes would gradually increase during the night and be greatest at the end of the swarm. But despite the greater number of males (a proportion of two males to one female, as noted by Mayer [1908] and substantiated in the present study) and despite the greater fragility of the female epitokes, which would prevent them from having as

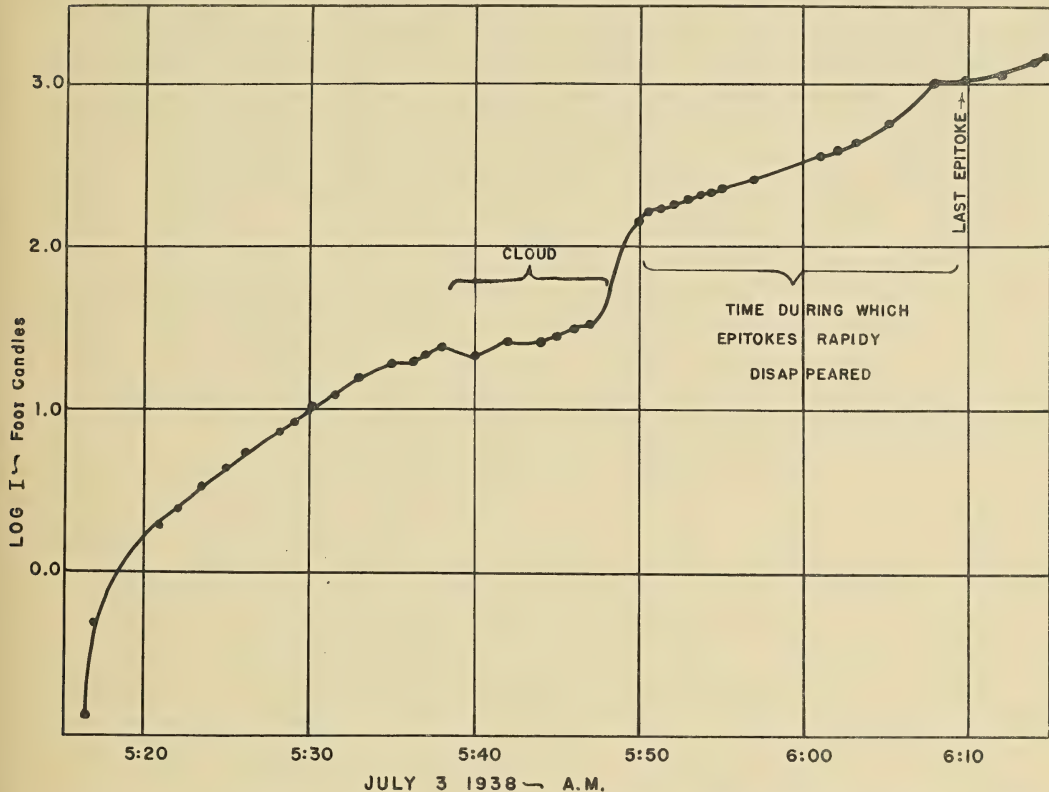


Fig. 5. Increase of intensity of daylight on the morning of July 3, 1938. Dots indicate individual readings of light intensity. From the first appearance of dawn, epitokes ruptured at an increasing rate until at 5:50 a.m. it reached a maximum. Epitokes rapidly disappeared until 6:09 a.m., when the last one was seen.

long an average free existence as the males, the number of females at 2:00 a.m. exceeded the number of males by some 45 per cent, and the excess continued until the end of the swarm. It is concluded that the males have a tendency to swarm before the females. The later appearance of the females may be an adaptation to their greater fragility. If the males and females swarmed simultaneously, the females might shed their eggs before many males had yielded sperm, and the chance of successful fertilization might be decreased. With the males tending to precede the females, the males would have more opportunity to be ex-

posed to stimuli inducing the shedding of sex products, and males and females would shed at more nearly the same time.

Swarming males and females were observed until 6:09 a.m., when the first shed its sexual products. Exhausted epitokes continued to swim until after 7:00 a.m., but soon thereafter sank to the bottom or were taken by actively feeding fish. The morning was calm and clear with a few clouds in a layer 5° above the horizon and a few wispy clouds a little higher.

At 4:30 a.m., the first streaks of dawn appeared. In view of Mayer's observations many times repeated (Mayer, 1908; Bullington, 1930 and elsewhere) that light from the rising sun induced shedding of the sexual products, light measurements were made from the time light intensities reached 0.135 foot-candle until after the last epitoke fragmented. Measurements were made with a photocell and Leeds and Northrup galvanometer, the photocell measuring incident light falling on its horizontal surface 10 feet above mean tide level.

The results are indicated in figure 4 and shown in greater detail in figure 5. With the first appearance of dawn the epitokes broke rapidly, but the last one did not rupture until the light intensity reached 1095 foot-candles, a difference of intensity of almost ten thousand fold. The difference in threshold intensity necessary to cause shedding of sexual products will be discussed elsewhere.

The swarm observed occurred on the night before the first quarter moon on July 4, 1938. On July 2 the sun set at 7:26 p.m., the moon set at 10:40 p.m., and the sun rose the next morning at 5:46 a.m. (E.S.T.). It should be pointed out that the swarm began before 9:15 p.m. on the evening of July 2, when the moon was still above the horizon.

The above observations on the course of a swarm vary in a number of essential details from those of Mayer (1908), perhaps the most important being the time relations of the swarm. He believed that the swarm began about 3:00 to 4:00 a.m. and persisted until after sunrise, with the individuals most numerous at sunrise. The above observations show that the swarm began about 9:30 p.m. and the maximum number of free-swimming individuals occurred about 3:30 a.m.

Although Mayer does not state so specifically, it may be inferred that his observations were made at the time of the third quarter moon, since he noted only two swarms at the first quarter and nine at the third quarter moon previous to the publication of his paper. If such is the case, then Mayer's results do not agree with ours in regard to standard time, but do show a certain agreement if the lunar cycle is taken into consideration. The first and third quarter moons are approximately similar in the intensity of moonlight and in time above the horizon at night. They differ in the part of the night when they are up. The first quarter moon is in the sky at sunset and sinks below the horizon at about midnight, with moonlight from sunset to midnight. The third quarter moon rises about midnight and is still above

the horizon at sunrise, giving light from midnight to sunrise. The swarm on the night of July 2, 1938, at the first quarter moon, began about 9:15 p.m., when the moon was shining. If Mayer's observations were correct, swarms at the third quarter moon did not begin until 3:00 or 4:00 a.m., when the moon would be above the horizon. Thus the observations agree in that swarming began after sunset and when the moon was above the horizon irrespective of the time when these conditions occurred. This suggests that the moon has a local and immediate influence on swarming. Mayer's (1908) observation that shading palolo for two nights inhibits swarming lends support to this view.

Attempts were made during 1939 to make observations on the onset and progress of a swarm at the time of the third quarter moon on July 9. A major swarm did not appear over West Loggerhead Reef, so observations are incomplete. However, it was possible to determine a time before which epitokes definitely appeared. A summary of positive results is given below:

Night of July 8-9, 1939

Sunset 7:26 p.m., sunrise 5:47 a.m.

Moonrise 11:38 p.m. Third quarter moon on July 9.

9:00 p.m. to 12:20 a.m., no eggs in tow.

1:00 to 1:30 a.m., one male epitoke.

Observations continued at half-hour intervals until 6:00 a.m. No further epitokes seen. Few eggs found in tow.

Night of July 9-10, 1939

Sunset 7:26 p.m., sunrise 5:47 a.m.

Moonrise 12:14 a.m.

8:30 to 11:00 p.m., no eggs in tow.

11:30 p.m. to 12:00 a.m., no epitokes seen.

1:00 to 1:45 a.m., two male epitokes.

No further epitokes seen. Few eggs in tow in morning.

Night of July 11-12, 1939

Sunset 7:25 p.m., sunrise 5:48 a.m.

Moonrise 1:37 a.m.

8:45 to 9:15 p.m., a few eggs in 1- and 2-cell stages in tow.

9:30 to 10:00 p.m., a few eggs in 2- and 4-cell stages in tow.

10:00 to 10:45 p.m., two male and one female epitokes.

11:15 to 11:45 p.m., no epitokes.

1:00 to 1:45 a.m., one male epitoke.

No more epitokes seen, although observations continued until 5:45 a.m. Eggs numerous in tow in morning. At 8:30 a.m. eggs were in 8-, 16-, and 32-cell stages.

Night of July 12-13, 1939

Sunset 7:25 p.m., sunrise 5:49 a.m.

Moonrise 2:24 a.m.

9:00 to 9:40 p.m., eggs in tow. One female epitoke at 9:20 and one male at 9:25 p.m.

Night of July 12-13, 1939--Continued

Eggs in tow during night but no more epitokes seen.

Eggs fairly numerous in tow in morning in 32- and 64-cell stages.

Night of July 13-14, 1939

Sunset 7:25 p.m., sunrise 5:50 a.m.

Moonrise 3:18 a.m.

7:30 to 8:30 p.m., no eggs in tow.

10:00 to 10:30 p.m., a few eggs in 1- and 2-cell stages in tow.

12:00 to 12:30 a.m., a few eggs in 8- and 16-cell stages in tow.

8:30 a.m., eggs in 64- and 128-cell stages numerous in tow.

On the nights of July 8-9 and 9-10 no epitokes were seen or eggs recovered in tow until after moonrise, but on the three other nights eggs in early stages and epitokes were seen before moonrise and about the same time in the evening as the onset of swarming under the influence of a first quarter moon.

The criticism may be made that the 1939 observations were not made on epitokes which were part of a major swarm, and therefore were not comparable with the 1938 observations. Nevertheless, the epitokes did appear at about 9:00 p.m. The authors believe that they were studying the incipient stages of a major swarm but that local conditions (see discussion of effect of wind conditions on swarming) arose to prevent swarming from reaching maximum proportions.

It is concluded that swarming begins early in the night irrespective of the position of the moon, and thus moonlight does not have a local and immediate influence as suggested above. This conclusion is in agreement with Treadwell's (1914) observations that the Atlantic palolo would swarm even if shaded for 24 hours before the date of the swarm, and Mayer's (1908) statement that swarming takes place even if the moon is completely obscured by dense clouds.

WIND CONDITIONS AS A FACTOR INFLUENCING SWARMING

The absence of a major swarm near the last quarter moon of July 1, 1937, the absence of abundant swarms in other places in the West Indies (Treadwell, 1914) where palolo worms are numerous, and particularly the differences in the behavior of the worms over West Loggerhead and Bird Key reefs in 1937, 1938, and 1939 (table 4), made it seem probable that factors other than lunar periodicity play an important part in determining the particular day on which swarming takes place.

Observations during the three years indicated that water turbulence or wave action may be one of these factors. The wave action and water turbulence over the two reefs considered is dependent mainly upon the velocity and direction of the wind. Therefore a study of the relation of wind direction and force to major swarms, 1898 to 1936, a comparison of conditions over West Loggerhead and Bird Key reefs as correlated

with swarming in 1937, 1938, and 1939, and detailed observations taken nightly from June 29 to July 16, 1939 should give information regarding the problem.

Records of wind direction and velocity at Key West, Florida, 68 miles east of the Dry Tortugas Islands, were procured for the days preceding and following the time of swarming for all years from 1898 to 1925. Similar data were procured for the Dry Tortugas from 1925 on. The data are summarized in table 6.

Table 6. Relation of swarming of the Atlantic palolo to wind conditions, 1898-1936

(Swarming data from table 2; meteorological data from the Weather Bureau, Key West, and the Lighthouse Service, Dry Tortugas Islands, Florida. Moon's phase: *F.Q.*, first quarter; *F.M.*, full moon; *L.Q.*, third quarter. Wind velocity in miles per hour.)

Year	Month	Day	Moon's phase	Swarming	Meteorological data - Key West			
					Wind velocity		Wind direction	
					8 a.m.	8 p.m.	8 a.m.	8 p.m.
1898.....	July..	9		yes	6	3	SE.	W.
		10	L.Q.	yes	9	4	S.	SW.
1899.....	June..	28			10	9	SE.	NE.
		29	L.Q.		8	3	SE.	S.
		30			4	2	S.	S.
	July..	1		yes	6	4	S.	S.
		2		yes	5	7	NE.	SW.
1900.....	July..	17			9	11	SE.	SE.
		18	L.Q.		9	9	SE.	SE.
		19		yes	9	4	E.	SE.
1902.....	July..	10			5	3	E.	SE.
		11	F.Q.		7	4	SE.	SE.
		12			7	4	E.	SE.
		13			6	5	SE.	E.
		19			7	9	SE.	E.
		20			9	9	SE.	E.
		21			5	5	SE.	S.
		24		yes	7	4	SE.	SE.
		25		yes	7	3	SE.	SE.
		26			5	4	S.	NE.
		27	L.Q.		7	7	E.	E.
		28		yes	9	6	E.	SE.
1903.....	July..	16			7	9	SW.	W.
		17	L.Q.	yes	5	6	SE.	W.
		18			6	6	W.	NW.

(Continued on following page)

Table 6 - *Continued*

Year	Month	Day	Moon's phase	Swarming	Meteorological data - Key West			
					Wind velocity		Wind direction	
					8 a.m.	8 p.m.	8 a.m.	8 p.m.
1905.....	July...	8			5	9	NE.	E.
		9	F.Q.	yes	7	5	SE.	SE.
		10		yes	13	7	S.	SE.
		11			9	9	S.	E.
		21		yes	8	9	NE.	S.
		22		yes	7	5	W.	SE.
		23		yes	7	12	E.	E.
		24	L.Q.	yes	12	16	E.	E.
1906.....	July...	9			9	5	E.	E.
		10			7	5	SE.	E.
		11		yes	7	6	SE.	N.
		12		yes	9	3	SE.	E.
		13	L.Q.	yes	7	7	SE.	SE.
1907.....	July...	1		yes	9	7	E.	NE.
		2	L.Q.	yes	10	7	SE.	E.
		3			13	10	SE.	SE.
1908.....	July...	4			10	10	E.	E.
		5			15	12	SE.	E.
		6	F.Q.		8	9	NE.	E.
		7			9	9	SE.	E.
		8			7	7	NE.	SE.
		9			2	8	SE.	SW.
		10		yes	2	4	SW.	SW.
		11			8	3	SE.	W.
		12			10	7	SW.	E.
		17			7	3	SE.	SE.
		18			8	4	SE.	SE.
		19	L.Q.		4	3	SE.	S.
		20			3	7	SE.	N.
1909.....	July...	21			9	9	W.	NW.
		5			9	5	SE.	E.
		6		yes	9	4	E.	E.
		7		yes	5	4	S.	N.
		8			10	12	N.	NW.
		9	L.Q.		12	9	NW.	NW.
1910.....	June...	10			9	12	W.	W.
		29	L.Q.	yes	5	6	S.	SE.
		30		-yes	9	14	S.	SW.

(Continued on following page)

Table 6 - Continued

Year	Month	Day	Moon's phase	Swarming	Meteorological data - Key West			
					Wind velocity		Wind direction	
					8 a.m.	8 p.m.	8 a.m.	8 p.m.
1911.....	July...	2	F.Q.		5	9	E.	NE.
		3			3	2	E.	N.
		4			3	2	E.	W.
		5			5	6	E.	E.
		6			10	12	NE.	NE.
		7			5	6	NE.	NE.
		8			7	9	E.	E.
		15			11	9	E.	NE.
		16		yes	8	9	E.	NE.
		17		yes	7	6	E.	E.
		18	L.Q.		9	5	E.	E.
		19			6	10	E.	N.
1912.....	July...	5			3	5	NW.	E.
		6		yes	5	6	E.	E.
		7	L.Q.	yes	6	8	E.	SE.
		8			9	7	SE.	E.
1914.....	July...	8			8	10	SW.	S.
		9			9	9	S.	E.
		10			7	2	SE.	SE.
		11		yes	9	9	SE.	E.
		12			7	3	E.	NE.
1915.....	June...	28			9	9	E.	NE.
		29			5	5	S.	SE.
		30			9	8	SE.	SE.
	July	1		yes	5	8	SE.	SE.
		2			5	8	SE.	SE.
		3	L.Q.		18	10	SE.	SE.
1916.....	July...	3			15	16	SE.	SE.
		4			21	16	SE.	SE.
		5			12	9	S.	SE.
		6			14	12	SE.	SE.
		7			8	9	SE.	E.
		8	F.Q.		6	3	SE.	SE.
		9			9	3	SE.	W.
		10			8	10	SE.	N.
		11			4	7	SE.	SE.
		12			2	4	W.	NE.
		13			3	8	NW.	NW.

(Continued on following page)

Table 6 - Continued

Year	Month	Day	Moon's phase	Swarming	Meteorological data - Key West			
					Wind velocity		Wind direction	
					8 a.m.	8 p.m.	8 a.m.	8 p.m.
1916 - cont....	July - cont.	14	F.M.	yes	3	8	NE.	SE.
		15			12	10	SE.	E.
		17			12	4	NE.	NE.
		18			8	6	SE.	SE.
		19			8	6	SE.	SE.
1922.....	June..	20	L.Q.	yes	8	4	SE.	NE.
		29			8	12	SE.	NE.
	July..	30			3	7	NE.	SE.
		1			7	8	SE.	SE.
		2	F.Q.		4	9	SE.	SE.
		3			9	6	SE.	SE.
		14			5	9	SE.	SE.
		15			13	13	SE.	SE.
		16		yes	12	7	SE.	SE.
		17	L.Q.		10	9	E.	SE.
1923.....	July..	5	L.Q.		9	9	E.	E.
		6			8	3	SE.	N.
		7		yes	5	3	SW.	N.
		8			6	8	SW.	NW.
1924.....	July..	4			10	8	SE.	SE.
		5			12	9	SE.	E.
		6			12	13	SE.	SE.
		7			12	9	SE.	E.
		8			10	12	SE.	SE.
		9	F.Q.		10	8	SE.	E.
		10			11	9	S.	NE.
		11			11	9	SE.	SE.
		19			9	9	NW.	NW.
		20			8	8	E.	SE.
		21			12	6	SE.	E.
		22	L.Q. (23)	yes	6	7	NE.	E.
				Meteorological data - Tortugas: Wind force and direction				
1925.....	July..	7			Fresh; NE.			
		8			Moderate; NE.			
		9			Light; SE.			
		10		yes	Fresh; NE.			

(Continued on following page)

Table 6 - Continued

Year	Month	Day	Moon's phase	Swarming	Meteorological data - Tortugas: Wind force and direction	
1925 - cont.,..	July - cont..	11			Fresh; E.	
		12	L.Q.		Moderate; E.	
		13			Calm	
		14			Fresh; SE.	
1929.....	June...	24			Moderate; E.	
		25			Light; E.	
		26			Light; E.	
		27			Light; E.	
		28		yes	Light; E.	
		29		yes	Light; E.	
		30	L.Q.	yes	Light; E.	
		July...	1		yes	Light; SE.
			2		yes	Light; SE.
			3		yes	Light; SE.
	4			yes	Light; NE.	
	5				Light; NE.	
	6				Moderate; NE.	
	1930.....	June...	13	F.Q.		
			14			Moderate; E.
			15			Moderate; E.
			16			Light; E.
			17		yes	Light; W.
			18		yes	Light; W.
			19			Moderate; S.
July...			27			Light; SE.
			28			Light; SE.
			29			Moderate; SE.
	30			Strong; E.		
	1			Moderate; E.		
	2			Light; E.		
	3	F.Q.		Moderate; E.		
	4			Light; E.		
	12			Light; SE.		
	13			Light; E.		
14			Light; E.			
15			Light; E.			
16		yes	Light; E.			
17			Light; NE.			
18	L.Q.					

(Continued on following page)

Table 6 - Continued

Year	Month	Day	Moon's phase	Swarming	Meteorological data - Tortugas: Wind force and direction
1931.....	July...	1			Light; E.
		2			Light; E.
		3			Light; E.
		4		yes	Moderate; SE.
		5			Light; E.
		6			Light; E.
		7	L.Q.		Light; E.
		8		yes	Light; N.
		9		yes	Light; W.
		10			Light; E.
1936.....	July...	5			Strong; NE.
		6			Fresh; E.
		7			Moderate; NE.
		8			Moderate; E.
		9			Light; SE.
		10		yes	Fresh; S.

Although the meteorological data from Key West are unsatisfactory, they constitute the only information available for the years in question. They must of course be used with discretion. Fortunately parallel data are available from both Key West and the Dry Tortugas after 1925, and a comparison shows that, in general, there is a correlation between the records of wind velocity and a fairly close correlation between the records of wind direction in the two locations.

There is no means of definitely ascertaining whether all records of swarming from 1898 to 1924 were made at West Loggerhead Reef. In the absence of any definite mention of Bird Key Reef or any note of differences in swarming over the two reefs, it is assumed that swarming would be observed over the more accessible reef. This would be West Loggerhead Reef, lying just beyond the dock of the Laboratory, a favorable point for early morning observation, rather than Bird Key Reef, 4 miles away.

If the above assumptions are correct, there is a correlation between swarming, as reported up to 1924 at the Dry Tortugas, and wind velocity. Swarming did not occur during the night following a day when the wind velocity reached more than 8 miles an hour. When the wind velocity reached 10 or 12 miles an hour for a few days, swarming did not occur until the wind had decreased for 2 or more days. If a large swarm appeared one night there was usually a second smaller swarm on the following night unless the wind increased in velocity to 10 or more miles

an hour, in which case swarming was not repeated the next night, e.g., July 10 and 24, 1905; July 8, 1909; July 15, 1916; etc. Thus the data indicate that there is a relation between swarming and the calmness of the water due to low wind velocity.

From 1925 to 1931 meteorological data from the Dry Tortugas can be more reliably correlated with swarming (table 6), but owing to the absence of an anemometer, the records of wind velocities are not exact. However, by the Beaufort wind scale, calm would indicate less than 1 mile per hour; light, 1-7; gentle, 8-12; moderate, 13-18; fresh, 19-24; and strong, 25-31 miles an hour.

In 1925, winds preceding the last quarter moon on July 12 were light to moderate and the worms swarmed 2 days before the quarter moon. In 1929, there was a period of light winds from the east or southwest from June 24 to July 4. Worms swarmed on successive days from June 28 to July 4, when the wind shifted to the northeast and increased to moderate on July 6. This caused turbulence over West Loggerhead Reef, and swarming ceased. At the time of the first quarter moon on July 13 the wind was moderate, and swarming did not occur again until July 17, when the wind decreased to light.

In 1930 a period of moderate to strong winds preceded the first quarter moon on July 3, and no swarming occurred at this phase of the moon. The last quarter moon of July 18 was preceded by a number of days with light winds, and swarming took place 2 days before the quarter, on July 16.

The conditions in 1931 are particularly significant. The period from July 1 to 4 was characterized by light winds, and swarming took place on the latter date, although the last quarter moon did not occur until July 7. On July 4, the wind increased to moderate and swarming ceased. Following a period of light winds on July 5, 6, and 7, swarming was reported again on July 8 and 9.

In the years 1925 to 1931 the particular day on which swarming occurred seems to have been determined by the pre-existing wind conditions.

During the summers of 1937, 1938, and 1939 careful observations supplemented by daily tows were made over West Loggerhead and Bird Key reefs. The results as related to wind conditions are given in table 7 and figures 6, 7, and 8.

The observations are much more comprehensive than the previous ones. Two areas were studied for comparison, and with the installation of an anemometer at the lighthouse on Loggerhead Key, wind velocity could be measured accurately. Consequently, conclusions drawn from these data are more accurate and should show more specifically the influence on swarming of water turbulence due to wind velocity.

In 1937, a major swarm was predicted and looked for at about the time of the last quarter moon on July 1. A southwest storm with a wind velocity of 20 miles an hour began on June 29 and lasted until July 12

Table 7. Showing relation of eggs recovered in tow to wind velocity and direction during 1937, 1938, and 1939

(L.Q., last quarter; F.Q., first quarter)

Year	Month	Day	Moon's phase	Swarming		Meteorological data - Tortugas:
				West Loggerhead	Bird Key	Wind velocity and direction
1937.....	June	25				4, E.
		26				6, NE.
		27				8, S.
		28				5, SW.
		29				10, SW.
		30				20, SW.
	July	1	L.Q.			15, S.
		2				15, S.
		3				10, E.
		10				10, E.
		11				10, E.
		12			Few	6, E.
		13		Few	Numerous	5, E.
		14		Few	Very abundant	4, NE.
		15	F.Q.	Few	Few	5, E.
		16		Fairly numerous		4, E.
		17		Few		3, SE.
		18				6, E.
		19				10, SE.
		20				10, SE.
		21				8, E.
		24				9, E.
		25				9, E.
		26				4, W.
		27		Numerous		11, S.
		28				10, S.
		29				7, SW.
		30				9, SW.
		31	L.Q.			9, SE.
	Aug.	1		Numerous		8, SE.
		2				5, NE.
		3				4, E.
		4				3, SW.
1938.....	June	15				6, NE.
		16				12, E.
		17				12, E.

(Continued on following page)

Table 7 - Continued

Year	Month	Day	Moon's phase	Swarming		Meteorological data - Tortugas: Wind velocity and direction
				West Loggerhead	Bird Key	
1938 - cont.	June - cont.	18				12, E.
		19				16, SE.
		20	L.Q.			14, S.
		21		Very few		Calm
		22		Fairly numerous		10, SW.
		23			Very few	5, W.
		24			Fairly numerous	9, E.
		25		Rare		12, E.
		26		Very few		8, E.
		27		Rare		6, SE.
		28		Few	Rare	2, S.
		29		Rare	Rare	8, W.
		30		Rare	Rare	4, SW.
	July	1		Rare	Rare	8, SW.
		2		Rare	Rare	Calm
		3		Very abundant	Rare	4, W.
		4	F.Q.	Very few	Rare	4, SW.
		5			Few	20, S.
		6				20, SW.
		7		Rare	Rare	6, SE.
		8			Rare	3, S.
		9			Fairly numerous	12, SE.
		10			Rare	14, NE.
		11		Very few	Rare	12, E.
		12				10, E.
		13			Rare	4, SE.
		14		Rare	Very few	4, SE.
		15		Very few	Very abundant	8, SE.
		16			Fairly numerous	4, E.
		17			Few	14, SE.
		18				28, E.
		19				22, E.
		20	L.Q.			14, E.
		21				14, E.
		22				10, SE.
		23		Rare		12, SE.
		24		Few		10, E.
		25				14, SE.
		26				12, SE.

(Continued on following page)

Table 7 - Continued

Year	Month	Day	Moon's phase	Swarming		Meteorological data - Tortugas: Wind velocity and direction
				West Loggerhead	Bird Key	
1939.....	June	17	N.M.			10, SE.
		18				12, SSE.
		19				10, E.
		20				10, SE.
		21				10, E.
		22		Rare		8, E.
		23		Few	Very few	5, NE.
		24	F.Q.	Few	Fairly numerous	10, NW.
		25			Very few	5, SW.
		26			Very few	Calm
		27		Numerous	Few	5, E.
		28		Few	Very few	4, S.
		29		Few	Rare	2, S.
		30		Numerous	Few	Calm
	July	1	F.M.	Abundant	Very few	Calm
		2		Fairly numerous	Abundant	3, S.
		3				3, SW.
		4		Rare	Rare	Calm
		5		Very few	Abundant	5, W.
		6			Very abundant	12, NW.
		7			Few	15, SW.
		8				15, S.
		9	L.Q.	Few	Few	12, S.
		10		Few	Rare	10, SW.
		11		Rare	Rare	10, SE.
		12		Numerous	Fairly numerous	5, E.
		13		Fairly numerous	Few	Calm
		14		Numerous	Few	5, W.
		15			Rare	15, W.
		16	N.M.			13, W.
		17				12, SW.
		18		Few		8, SW.
		19		Few	Fairly numerous	6, SE.
		20		Few	Rare	16, SW.
		21				17, SE.
		22				14, SE.
		23				16, SE.
		24				20, SE.

with the wind veering to the east. The wind dropped to 6 miles an hour on July 13, and a few eggs were found over Bird Key Reef. Eggs may have been present over West Loggerhead but were not found. The next day few eggs were found over West Loggerhead but they were numerous over Bird Key Reef. On July 14 the wind shifted to the northeast, with the result that Bird Key Reef was sheltered and West Loggerhead ex-

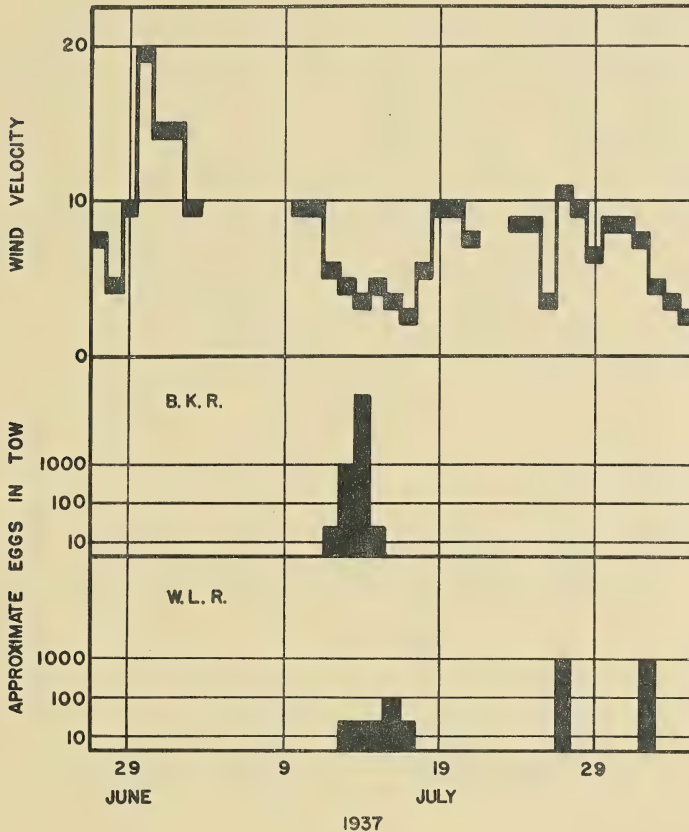


Fig. 6. Relation of swarming of the Atlantic palolo, *Leodice fucata*, to wind velocity in 1937. B.K.R., Bird Key Reef; W.L.R., West Loggerhead Reef.

posed. A major swarm occurred over Bird Key Reef, with eggs forming windrows several hundred yards long and many yards wide by midmorning, but only a few eggs were recovered over West Loggerhead. During the next day the wind shifted to the east and a few eggs were recovered over each reef. Sexually mature worms had all swarmed by July 15 over Bird Key Reef, for no eggs were recovered during the rest of the summer, nor were sexually mature palolo found in rocks (see table 5).

With continued light winds the next day from the east, eggs were fairly numerous on July 16 and few on July 17 over West Loggerhead Reef.

Although wind conditions were favorable, the swarming stimulus was lacking, and no eggs were found until July 27. Swarming was to be expected about the time of the full moon of July 23 (see July 14, 1916, table 2), but wind apparently prevented swarming. The wind slowly decreased until on July 26 it was only 4 miles an hour. On July 27 numerous eggs were found in tow. The same day, the velocity of a south wind increased to 10 miles an hour, and no swarm occurred on the next

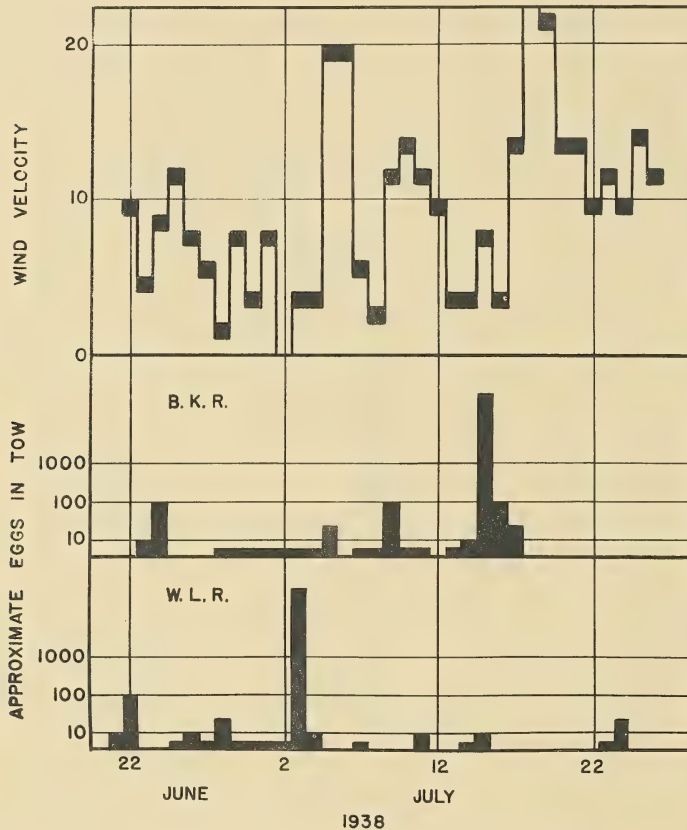


Fig. 7. Relation of swarming to wind velocity during 1938.

or the 3 succeeding days, July 29, 30, and 31. On the 29th and 30th the wind was in the southwest, so the water over West Loggerhead Reef was choppy. On the 31st the wind veered to the southeast, West Loggerhead was protected, and during that night some swarming took place, as shown by eggs in tow on August 1.

It is obvious that in 1937 the palolo swarmed around the quarter moon phases, but only when wind velocity was low or the reefs on which the worms were studied were protected from wind action.

During 1938 a similar condition existed. A strong east and south-east wind before the last quarter moon on June 20 probably prevented

swarming over both reefs.⁵ On June 20 the wind veered to the south so that West Loggerhead was protected, and the next morning a few eggs were found in tow. June 21 was calm, and eggs were numerous on June 22. During the day a strong southwest wind blew, so that West Loggerhead Reef was exposed. No eggs were found during the next 2 days over the reef. On June 23 a very few eggs were taken over Bird Key Reef, it being protected from a 5-mile west wind. On the next morning, June

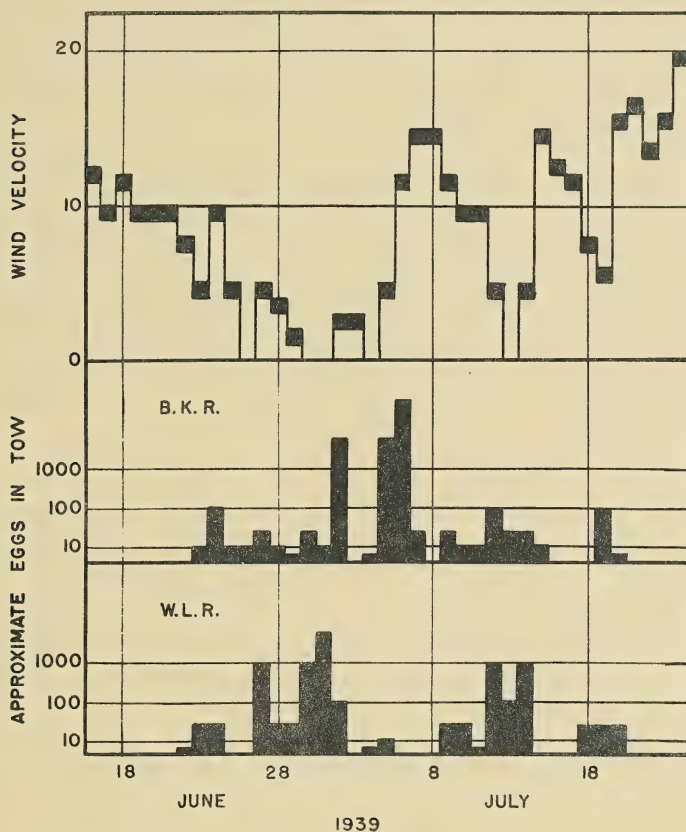


Fig. 8. Relation of swarming to wind velocity during 1939.

24, eggs were fairly numerous. During the period of the new moon on June 27, although wind conditions seemed satisfactory for swarming, eggs were rare over both reefs. On July 2 there was a calm, and the next night a major swarm occurred over West Loggerhead, the day before the first quarter moon of July 4. Except for small numbers of eggs appearing sporadically, usually after a few days of light wind, swarming ceased over West Loggerhead Reef.

⁵The reproductive products of worms on Bird Key Reef may have been immature at that time. See discussion under "Maturity as a Factor Influencing Swarming."

Although wind conditions seemed suitable for the occurrence of a major swarm over Bird Key Reef on July 3 or 4, no swarm materialized. The possibility of other factors preventing swarming will be discussed later. Wind conditions on July 5 and 6 were distinctly unfavorable, with a 20-mile south and southwest wind making the water at Bird Key Reef extremely choppy. No eggs were found on the morning of July 6 and they were rare on July 7. On July 7 and 8 the wind moderated, and the improved condition was reflected in the recovery of a fairly large quantity of eggs on July 9. Then the wind increased to 10 to 14 miles an hour until July 13. Eggs were rare on the 10th, 11th, and 13th and absent on the 12th. On July 13 and 14 the wind moderated to 4 miles an hour and on the latter night a major swarm occurred. The eggs were as numerous as on the morning of July 14, 1937 over Bird Key Reef, and the swarm resembled those described by Mayer (1908), Grave and Burkenroad (1929), and others. On July 16 new eggs were fairly numerous. On July 17 there were a few eggs. From July 17 until July 26, when the authors left the Laboratory, heavy winds blew from the east or southeast. It seems particularly significant that no eggs were recovered, although on July 23 a few sexually mature individuals were broken out of rocks. The fate of other such individuals was undetermined.

During 1939 observations were continued and extended. From before June 15 until June 21 wind velocity exceeded 9 miles an hour. No eggs were found. The first eggs during 1939 were secured on June 22 over West Loggerhead Reef, with an 8-mile wind. The next day eggs were found over both reefs. The wind dropped to 5 miles and came from the northeast, so West Loggerhead was exposed and Bird Key Reef was protected. On the next day, June 24, the day of a first quarter moon, eggs were few over West Loggerhead but fairly numerous over protected Bird Key Reef. During the same day the wind increased to 10 miles and veered to the northwest. Reproduction ceased over West Loggerhead and very few eggs were found over Bird Key Reef on June 25 and 26, although the wind dropped. On June 27 eggs were numerous over West Loggerhead although few were secured from Bird Key Reef.

From June 27 until the morning of July 6, general wind conditions were almost ideal for swarming. However, except for the taking of abundant eggs over West Loggerhead Reef on July 1, the day of the full moon, and over Bird Key Reef on July 2, the worms reproduced in limited numbers until July 5, when eggs were again abundant over Bird Key Reef, and July 6, when a tremendous swarm occurred over the same area, 3 days before the last quarter moon of July 9. The same day a 12-mile northwest wind arose, continuing from the southwest, south, and southeast, until July 11, during which time eggs were few or rare. On July 12 the wind dropped to 5 miles and eggs were numerous over West Loggerhead Reef and fairly numerous over Bird Key Reef. With calm weather on July 13 and a 5-mile wind on July 14, eggs were fairly numerous on the 13th and numerous on the 14th. A 15-mile wind on July 15, slightly decreasing to 13 and 12 miles on July 16 and 17, may have been the

cause of the lack of eggs over both reefs on July 16 and 17 and their rarity over West Loggerhead Reef on July 18. On July 18 and 19 the wind decreased to 6 miles an hour, and, although few eggs were taken over West Loggerhead Reef, they were fairly numerous on July 19 over Bird Key Reef. A small number of eggs were found over both reefs on July 20. From the latter date until the close of observations on July 24, strong winds prevailed and no eggs were found.

In addition to the general changes in wind velocity, it was felt that local changes of short duration may have had some effect on swarming. The following observations on reproduction as related to sudden wind changes show their importance:

Night of July 8-9, 1939

On the morning of July 8 a brisk south wind veered to the east and dropped about 4:00 p.m. The water was quite calm until 9:30 p.m., when a rain and wind squall blew up from the south. About 11:00 p.m. the wind dropped again and the water became less choppy. At 1:00 a.m. a single epitoke was seen and tow gave a few eggs. At 2:30 a.m. a brisk wind from the south continued for the rest of the night. Tows at 5:00 to 5:15 a.m. gave only a few eggs.

Night of July 9-10, 1939

July 9 had a brisk wind from south, water choppy. From 8:30 to 9:00 p.m. wind decreased but no eggs in tow. Between 9:30 and 10:15 p.m. wind freshened and no eggs in tow. 10:30 p.m. to 1:00 a.m. wind dropped considerably, water less choppy. At 1:00 a.m. saw two male epitokes and took few palolo eggs in tow. After 1:30 a.m. wind increased considerably and no more epitokes were seen. At 8:30 a.m. of the morning of July 10 few eggs in 4- to 16-cell stage in tow.

Night of July 11-12, 1939

During the morning of July 11 a moderate southeast wind dropped so water was only slightly ruffled. Towed 8:45 to 9:15 p.m., found few palolo eggs in 1- and 2-cell stages and at 9:30 found some with 2 and 4 cells. About 8:30 p.m. wind freshened from the north and water gradually grew choppy. Wind continued and water grew rougher until 4:00 a.m., when wind decreased and veered to the east. After 10:30 p.m. four swimming epitokes were seen, the last at 1:00 a.m., although observations were continued until 5:45 a.m. At 8:30 a.m. eggs in 8-, 16-, and 32-cell stages were numerous in tow.

Reproduction began early in the evening but with an increasing north wind, and swarming stopped about an hour after midnight when the water became quite choppy. Although the wind decreased after 4:00 a.m., no further swarming took place, as indicated by the absence of eggs in 1-, 2-, or 4-cell stages in the morning tow.

Night of July 12-13, 1939

The gentle east wind of the morning increased and veered to the northwest and water was choppy. Between 9:00 and 9:40 p.m. wind somewhat less.

Towed 9:00 to 9:15 p.m. and found few eggs in tow. At 9:20 and at 9:25 p.m. saw one epitoke. At 11:00 p.m. wind freshened and no further epitokes were seen. The wind died down toward morning but apparently no epitokes swarmed in the latter part of the night, as there were no eggs with less than 32 cells in the morning tow.

The above observations show that a change of wind velocity of short duration, too local to be recorded in meteorological data, may have an effect on swarming. These local changes in wind direction and velocity may have prevented swarming in past years on days when weather records indicate that favorable conditions existed, e.g., June 30, 1899; July 10, 13, 1902; July 19, 1908; July 10, 1914, etc.

The present investigation showed that during 1937, 1938, and 1939, wave action prevented swarming if the wind velocity exceeded 8 miles an hour on the day before the swarm unless the reef was protected (table 8; figs. 6, 7, 8). Differences in amount and time of swarming over Bird Key and West Loggerhead reefs were due to differences in exposure of the reefs to wind action.

MATURITY AS A FACTOR INFLUENCING SWARMING

The records in tables 2 and 4 show that June 28⁶ is the earliest date on which major swarms are noted and July 28 the latest. Table 8 gives the ratio of the number of swarms to the first and third quarter phases of the moon for successive 5-day periods between June 28 and July 27 for those years from 1898 to 1939 for which swarming records are available. The ratio increases to a maximum about the 8th of the month and then begins to decrease. This can be interpreted to mean that palolo tends to swarm after the quarter moon during the first part of July and to swarm before the quarter moon during the latter part of the month, indicating that as the season advances there may be changes in the animals making them more sensitive to the stimulus initiating swarming. This may be the reason why worms do not swarm to the stimulus of the first quarter moon when it occurs in the early part of July, but may swarm if it occurs later, although the first quarter moon may be subsequent to dates on which worms had swarmed in other years in conjunction with the third quarter moon. In 1910 and 1929 palolo swarmed on June 29 and 30 on last quarter moons, but since 1898 the first quarter moon has occurred nine times between June 28 and July 5 with only a single swarm recorded, on July 3, 1938, over West Loggerhead Reef but not over Bird Key Reef.⁷ However, a first quarter moon on July 6 or

⁶ In 1938 freshly laid eggs were found (table 4) on June 21 and for some days thereafter. Some few worms may anticipate the above date.

⁷ It should be remembered that there was no major swarm over West Loggerhead Reef in 1937.

later may result in a swarm, as for example in 1906, 1908, and 1929. In 1905 the first quarter moon occurred on July 9 and swarms occurred on the 9th and 10th; in 1908 a swarm occurred on July 10 with the first quarter on July 6; and in 1939 swarms occurred on July 17 and 18 with a first quarter moon on July 13. But in 1902, 1910, 1916, and 1924 there were first quarter moon phases on July 11, 13, 8, and 9 respectively without record of swarming. The year 1910 is somewhat exceptional in that swarms had occurred previously on June 29 and 30 at the

Table 8. *Showing the relation of all swarms recorded from 1898 to 1936 to the occurrence of the third quarter moon phase during successive five-day periods from June 28 to July 27*

5-day period	No. swarms	No. times third quarter moon occurred within period	Ratio
June 28 - July 2.....	11	5	2.2
July 3 - July 7.....	9	3	3.0
July 8 - July 12.....	12	4	3.0
July 13 - July 17.....	8	4	2.0
July 18 - July 22.....	7	5	1.4
July 23 - July 27.....	4	3	1.33

third quarter on June 29. However, in 1929 an almost comparable condition existed, with a third quarter moon on June 30 and swarming on June 28, 29, 30, July 1, 2, 3, and 4, but other swarms were produced on July 17 and 18 after the first quarter moon on July 13.

It would seem from these data that palolo will not swarm until they have reached a certain stage of maturity and that after they have passed this period, they respond to the first suitable moon phase if other conditions are favorable.

If it is postulated that the first quarter exerts less stimulus on swarming than the third quarter moon, then it is reasonable to suppose that palolo might be ready to respond to the third quarter but not to the lesser stimulus of the first quarter at any particular date early in the summer. If it be further postulated that there may be slight variation in rate of maturity from year to year, it would be reasonable to suppose that on occasion the rate of maturity would lag and during the same years the worms would not be ready to react to the stimulus of the first quarter moon early in July.

The most general measure of the state of maturity at any date would be the time lapse since the previous year's swarming. If the worms swarmed early one year they might be ready to yield a dense swarm on the first quarter moon the next year, and, conversely, if they swarmed late one year, they might not be quite ready to swarm on the first

quarter the following year. Such a theory is partially substantiated by the records. In 1907 (table 3) swarms occurred early, on July 2 and 3. In 1908 a swarm occurred on July 10 near the first quarter. In 1915 a swarm occurred even earlier, on July 1 at the third quarter, and in 1916, although no swarm occurred on the first quarter, a dense swarm occurred on July 14 at the time of the full moon. Over Bird Key Reef a swarm occurred on July 10, 1936, and the next year a swarm occurred on July 14, one day before the first quarter moon.

In general, if palolo worms swarm early one year they may swarm on a first quarter moon the next. Conversely, if swarming occurred later in the preceding year or the first quarter is relatively early, there is very little likelihood of swarming occurring at that time. Table 9 is a summary of all records, 1898 to 1939, with the dates of the quarter moons occurring between June 28 and July 25, the date of the major swarm, the lapsed time in days from the swarm of the previous year to the quarters, and the lapsed time from the major swarm of the previous year to the swarm of the year under consideration. Certain relationships appear. The shortest time between major swarms in successive years is 353 days in 1905-1906, 1924-1925, and 1936-1937. The longest intervals are 383 days in 1899-1900 and 385 days in 1929-1930. No swarm has been recorded as occurring at the first quarter moon if the major swarm of the year before took place less than 369 days previously, e.g., 1936-1937 at Bird Key Reef. A decrease of even 2 days seems to prevent swarming, e.g., 1910-1911. With the exception of the situation at Bird Key Reef in 1937, which will be discussed later, the major swarms at the first quarter always occur after the quarter and subsequent swarms always occur at the next third quarter.

A major swarm occurred over Bird Key Reef on July 14, one day before the first quarter moon, with no swarming about the previous third quarter moon on July 1, although 356 days had elapsed since the swarm of the previous year. This demands comment. The high winds blowing continuously from June 24 to July 3, with the resulting ground swell, effectively prevented swarming. But swarming occurred on July 14, one day before the first quarter moon and 369 days after the swarm of the previous year. This is in essential agreement with past records, which show that swarming did not take place on a first quarter moon less than 369 days after the swarm of the previous year. This case is exceptional in that it is the only one on record where swarming did not take place about the time of a third quarter moon in July and a major swarm occurred before the next first quarter. This condition seems to have been due to the continuous high winds prevailing about the first of the month.

In 1938 a particularly anomalous condition seemed to be present. The weather conditions for the day of the first quarter moon of July 4 and the two previous days were particularly favorable for swarming over both West Loggerhead and Bird Key reefs (table 4). A major swarm oc-

curred over West Loggerhead Reef on July 3 but eggs were rare over Bird Key Reef. The time lapse was only 354 days after the 1937 swarm over Bird Key Reef. The absence of a swarm over that reef supports previous findings that swarming will not take place on a first quarter moon in less than 369 days after the swarm of the previous year. But a major

Table 9. *Showing the relation of the major swarm in any one year to number of days which have elapsed from the major swarm of the previous year and to the first and third quarter moon phases occurring after June 28*

(Data from tables 2 and 4. B.K.R., records from Bird Key Reef)

Year	Date of quarter moon phases after June 28		Date of swarming at 1st quarter	Date of swarming at 3d quarter	No. days from major swarm of previous year to major swarm at 1st quarter	No. days from major swarm of previous year to major swarm at 3d quarter
	1st quarter	3d quarter				
1898-99.....	July 15	June 29		July 1		357
1899-1900....	July 4	July 18		July 19		384
1902-03.....	July 3	July 17		July 17		358
1905-06.....	June 29	July 13		July 12		353
1906-07.....	July 18	July 2		July 2		355
1907-08.....	July 6	July 19	July 10	July 19		382
1908-09.....	July 24	July 9		July 6	373	361
1909-10.....	July 13	June 29		June 29		358
1910-11.....	July 2	July 18		July 16		382
1911-12.....	July 21	July 7		July 6		355
1914-15.....	July 19	July 3		July 1		355
1915-16.....	July 8	July 21	July 14	July 20	382	388
1922-23.....	July 20	July 5		July 7		358
1923-24.....	July 9	July 23		July 22		381
1924-25.....	June 29	July 12		July 10		353
1929-30.....	July 18	July 3		July 16		371
1930-31.....	July 22	July 7		July 4		353
1936-37 B.K.R.	July 15	July 1	July 14		369	
1937-38 B.K.R.	July 4	July 20		July 15		366
1938-39 B.K.R.	June 23	July 9		July 6		356

swarm did take place over West Loggerhead Reef. Unfortunately, there is no point of reference for 1937 over West Loggerhead, as a major swarm was not observed. The majority of worms may have swarmed some time previous to July 1, 1937, though this seems improbable, as numbers of mature worms were broken out of rocks on July 4 (table 5).

In 1939 the behavior of the worms over Bird Key Reef was in accordance with observations of the previous years. A major swarm occurred

358 days after the major swarm of the previous year and 3 days before the last quarter moon on July 9, after a period of relative calm. But over West Loggerhead Reef no major swarm occurred. At the last quarter moon of July 9 there had been a lapse of 370 days since the swarm of the previous year and a swarm was confidently expected. But on the night of July 6-7, when the worms swarmed over Bird Key Reef, a north wind arose and the water over West Loggerhead became choppy, a condition which may have prevented swarming over this reef, while the former was protected.

In summary, it has been found that during the early part of July palolo tends to swarm after the quarter moon, while during the latter part of the month it tends to swarm before the quarter (table 8). During some years, at quarter moon phases occurring early in July and with weather conditions seemingly suitable, no major swarm materialized. In all such cases less than 353 days had elapsed from the swarm of the previous year if it was a third quarter moon, or less than 369 days had elapsed if a first quarter moon. With one exception (1937) the worms always swarmed after the first quarter moon, and with one exception (1937), if they swarmed on the first quarter, they always yielded another large swarm on the next third quarter. This is in accordance with the theories that the third quarter moon is a more effective stimulus to swarming than the first quarter moon and that the sensitivity of the worms to stimuli inducing swarming increases with maturity. It seems probable that the stage of maturity is a factor influencing the time of swarming.

OTHER FACTORS POSSIBLY INFLUENCING SWARMING

Various other climatic and environmental conditions were investigated. Among these were tides, cloudiness at night, temperature, and the hydrogen-ion concentration of the water, all factors which influence reproduction in some animals; but the results were not significant.

Friedlaender (1898) believed that the Pacific palolo, *Eunice viridis*, swarms as a result of negative geotropism through diminished water pressure at low tides. Izuka (1903) claimed that in the Japanese palolo (*Ceratocephale osawai*) swarming invariably takes place just after the flood tide in the evening. This would suggest that tides might play some part in swarming in the Atlantic palolo, but no direct relation could be found between tides and swarming. Mayer (1908) pointed out that worms in rocks placed in floating live cars and consequently not subject to tidal action swarmed at the normal time. The state of the tide may have some influence on water turbulence induced by wind action, but this would be slight at the Dry Tortugas Islands.

Except for whatever influence temperature has on the rate at which the worms mature, it seems to have no significant effect in determin-

ing the particular day on which swarming occurs under the conditions existing at the Dry Tortugas Islands.

Cloudiness at night was considered by Mayer (1908), but he eliminated it as a factor when he observed that worms swarmed when the moon was completely obscured.

McClendon (1917), in a series of extensive studies, found "no relation between pH and location, time or tide" at the Dry Tortugas.

DISCUSSION

The observations on swarming of the Atlantic palolo made during 1937, 1938, and 1939 show that reproduction is not exclusively restricted to periods centering about the first or third quarter moon phases, as Mayer concluded, but may occur sporadically at almost any time during the moon's cycle except at the new moon. However, there is usually a significant increase in swarming at the first or third quarter phase of the lunar cycle. Major swarms, during which many more worms reproduce than at all other times together, always occur within 5 days of the quarter moon with the one exception noted, that on the full moon in 1916. Consequently, in a consideration of the general problem of the swarming of this worm, it is proposed to confine attention to the major swarms except when the minor ones yield information pertinent to the analysis of the factors involved.

The moon's phases undoubtedly are significant. Swarming about the quarter moon phases may be due to inhibition at other periods of the lunar cycle or may be due to a stimulus exerted at the quarters and not at other times. The end results would be essentially the same, but until more information is available, no decision can be made as to the mechanism by which lunar cycles influence swarming. However, the actual presence of moonlight is not necessary to initiate swarming (see "The Course of a Swarm"), so the series of events resulting in swarming must be influenced by the moon before that time. It is significant that the only swarm definitely reported elsewhere than at the Dry Tortugas occurred at Andros Island in the Bahamas on June 12, 1914, 3 days before the moon's last quarter. Although the worms swarmed a month earlier there than at the Dry Tortugas, they showed the same relation to the lunar cycle.

The influence, possibly stimulatory, exerted by the first and third lunar phases seems to differ in intensity in the two quarters. Reports are rare of swarming at the first as compared with the third quarter moon; swarming has taken place many times at the third quarter moon on dates preceding the date of the earliest recorded swarm on the first quarter. In no case has swarming occurred at the first quarter less than 369 days from the swarm of the preceding year, while worms have swarmed at the third quarter moon at 353 days (see "Maturity as

a Factor Influencing Swarming"). These considerations are in harmony with the idea that the third quarter moon has a greater positive effect on swarming than the first quarter moon and with the idea that the worms grow increasingly sensitive to stimuli inducing swarming, even after the sexual products are mature.

If all other factors are favorable, then the date of swarming is the date of the quarter moon whose stimulus is sufficient to cause the worms to respond, a condition depending not only upon the moon quarter but also upon the sensitivity of the worm.

If worms after 353 days from the last annual swarm can be stimulated to swarm by a third quarter moon, and after 369 days by a first quarter moon, the increase in sensitivity during the interval must balance the decreased intensity of the stimulus of the first quarter.

If only the two factors of relative stimulation efficiency of the first and third quarter moons and maturity were involved, swarming could be predicted as follows: Swarming would take place at the time of the first quarter moon occurring more than 369 days from the date of swarm of the previous year or at the time of the third quarter moon occurring more than 353 days from the swarm of the previous year. In any one year the worms would swarm at the phase of the moon first fulfilling these requirements, provided other conditions were favorable.

Among the other conditions which must obtain is quiet water. Wave action and water turbulence, as influenced by wind velocity and direction, prevent swarming at the Dry Tortugas Islands if the wind has a velocity greater than 8 miles an hour, unless the water is sheltered. Even after a swarm has begun wind may cause sufficient wave action to cause its cessation. Wind, or rather the resulting water turbulence, seems to be an important inhibitory factor in swarming, important enough, in fact, to prevent swarming completely (July 1, 1937) although other conditions seem satisfactory.

Tides, to the extent that they induce or modify currents or change the depth of water and consequently contribute to water turbulence occasioned by wind, may play some part in determining swarming. Otherwise there is no evidence that change of water level, hydrostatic pressure, etc., caused by tides, influence swarming.

It seems that the most important factors determining the time of swarming in the Atlantic palolo are the lunar cycle, the maturity of the animal, and the amount of water turbulence.

SUMMARY AND CONCLUSIONS

As first approximations, Mayer's (1908) conclusions that the reproductive period of the Atlantic palolo is very limited and that reproduction occurs between June 28 and July 26 within 4 days of the third quarter moon, unless the phase occurs late in July, when there may be

swarming on the first quarter moon, are correct. In years when major swarms occur, a large majority of the worms do reproduce on the same night, usually within 5 days of the quarter moon phase. Swarming data recorded since, with observations made during 1937, 1938, and 1939 at the Dry Tortugas, yield additional information and allow extension and modification of Mayer's conclusions. The results may be summarized as follows:

1. Worms may swarm sporadically and in small numbers at any phase of the lunar cycle except on or about the time of the new moon, from June 21 to August 1.

2. A major swarm may not materialize but a series of minor swarms may occur, e.g., West Loggerhead Reef in 1939.

3. If a major swarm appears, it usually occurs within 5 days of a quarter moon phase.

4. Worms, as they mature, show a change in the region of highest respiratory activity from the anterior end of the worm to the posterior end of the epitoke.

5. Worms begin to swarm before 9:30 p.m. at the first quarter when the moon is above the horizon, and at about the same time at the third quarter when the moon is below the horizon.

6. Swarming males appear to reach a maximum earlier in the night than the females.

7. Swarming epitokes were observed swimming on the morning of the swarm until morning sunlight reached an intensity of 1095 foot-candles.

8. The date of heaviest swarming is not simultaneous over a wide region. In 1938 it occurred on July 3 over West Loggerhead Reef and on July 15 over Bird Key Reef.

9. Weather data from Key West from 1898 to 1925 and from Dry Tortugas from 1925 to 1936 indicate, in general, that the swarming takes place only at a time of calm or low wind velocity, unless the water is protected.

10. Information from a comparison of swarming over Bird Key and West Loggerhead reefs in 1937, 1938, and 1939, correlated with observations of wind conditions, shows that swarming does not occur if wind velocity is greater than 8 miles an hour unless the reef is protected. This prevention of swarming is believed to be due to wave action and water turbulence.

11. Differences in amount of swarming can be accounted for by considering differences in the protection afforded the waters of the two reefs.

12. Although swarming may have begun, increase in wind velocity prevents its continuation.

13. Records accumulated from 1898 to 1939 show that worms never swarm less than 353 days after the swarm of the previous year at the third quarter, or less than 369 days at the first quarter.

It is concluded that:

1. Although reproduction occurs over a much longer period than was previously held, it is thought that the lunar cycle, maturity of the palolo worm, and wave action are the three main factors determining the time of a major swarm.

2. The stimulating effect of the first quarter moon is less than that of the third quarter moon, as shown by the fact that palolo will not swarm at the first quarter until after developing for 369 days from the swarm of the previous year, while they will swarm at the third quarter after 353 days.

3. This also indicates that the worms increase in sensitivity to the stimuli inducing swarming as they become sexually mature, and continue to do so after the sexual products are ripe.

4. Wave action and water turbulence above a certain level induced by wind will decrease or prevent swarming. The limiting amount of wave action is that effected by a wind of about 8 miles an hour under the conditions obtaining at the Dry Tortugas.

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III

THE REACTIONS OF THE ATLANTIC PALOLO,
LEODICE FUCATA, TO LIGHT

By LEONARD B. CLARK
Union College

and WALTER N. HESS
Hamilton College

With two text figures

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THE REACTIONS OF THE ATLANTIC PALOLO, *LEODICE FUCATA*, TO LIGHT¹

INTRODUCTION

The Atlantic palolo worm, *Leodice fucata*, is normally found in crevices and burrows in dead coral or limestone beach rock from the lower levels of the intertidal zone to 150 fathoms. At certain times of the year, usually at the first or third quarter moon phases, the posterior sexual portions of the worms (the epitokes) back out of the burrows, break away from the anterior asexual portions (the atokes), and swim to the surface. This is known as swarming. Sometimes swarming reaches immense proportions and the surface of the ocean is covered with swimming epitokes.

Mayer (1902), Treadwell (1914), and others noted that the atokal region of the worm was negative to light, while the free-swimming epitoke was positive. Mayer (1908, 1909) found that sexually mature worms shaded from moonlight for 2 or more days were prevented from swarming, but noted that under natural conditions, worms would swarm if the moon was completely obscured by clouds. Treadwell (1909) showed that shading worms for 24 hours from moonlight did not prevent swarming, while Clark and Hess (1939, 1940) found that swarming may occur several hours before moonrise.

Light is also a contributing factor (Mayer, 1900, 1902; Treadwell, 1909; Bullington, 1930) to the rupture of the epitokes and the release of the sex products.

No exact observations were made on the reactions of the worms to light until Hess (1931) showed that the worms are negative to all ordinary intensities of light but positive to very weak intensities; that if the brain is removed, they are negative to low illuminations to which they are normally positive, indicating that the brain functions in the positive response; and that the removal of the eyes, provided the underlying brain tissue is not injured, apparently does not affect the reaction to light. Hess suggested that the eyes may function as a visual organ rather than a photoreceptor. He also found that all segments are sensitive to light, but that the segments are light-sensitive only on the median dorsal and lateral regions except at the extreme ends of the body. The segments are not sensitive to light in the marginal regions between segments, or on the ventral surface except in the anterior and posterior region.

As the swarming season approaches, Hess found that the caudal end of mature worms becomes positive to low illuminations and when sev-

¹The authors wish to express their thanks to the Carnegie Institution of Washington for the opportunity to work at the Tortugas Laboratory, and especially to Professor David H. Tennent, Executive Officer of the Laboratory, for continued interest and assistance in the work.

ered from the asexual anterior portion swims toward a weak light in a spiral path.

The peculiarly complex opposed behavior in the two parts of the worm, the spectacular effect of light on the shedding of sex products, and the well-known occurrence of swarming of the worm at certain phases of the lunar cycle in July lend additional importance to a study of the light reactions of this form.

At the Dry Tortugas, Florida, one of the authors had opportunity to study the light reactions while carrying on experiments on swarming (Clark, 1937). Both authors continued the study in 1938 and 1939 in conjunction with further studies and observations on swarming (Clark, 1938, 1939; Clark and Hess, 1938, 1939).

LIGHT SOURCES

All observations on the light reactions were made in a darkroom or in the laboratory on dark nights after all illumination except the test lights had been extinguished. Observations made before 10:00 p.m. were usually made with a 100-watt, 110-volt Mazda lamp, the intensity being controlled by a calibrated Wratten neutral tint wedge and neutral tint filters, giving a range of 1:100,000 in intensity. After 10:30 p.m., 50-watt, 32-volt lamps were used. A variable resistance in the line prevented gross fluctuations in voltage. The light intensity of the experimental source was checked constantly with a photocell and a Leeds and Northrup portable galvanometer. It is believed that the intensities given are accurate to within 10 per cent.

LIGHT REACTIONS OF IMMATURE WORMS

Immature worms taken from their burrows were placed in square glass aquaria in the darkroom for 6 hours' dark adaptation. They were then tested in the aquarium with a horizontal beam of light of low intensity which was supported over a red light, so dimmed that the silhouette of the worm could just be distinguished and its movements ascertained.

The illumination was gradually increased until the animals responded. In 27 observations, the threshold for the positive response varied from 0.0007 to 0.0015 foot-candle, with an average of 0.001 foot-candle.

As the intensity increased, the animals gradually became negative, the threshold of the response varying from about 0.008 to 0.019 foot-candle, with an average of 0.01 foot-candle.

The anterior two-thirds of 15 of the worms was severed from the posterior third. The caudal pieces did not respond until the light in-

tensity was increased to approximately that required to cause the worms to give a negative response.

REACTIONS OF MATURE WORMS AND SEPARATE ATOKES AND EPITOKES

Owing to the great difficulty of procuring complete sexually mature worms (Clark and Hess, 1940), only 17 complete worms were tested during the 18 weeks in which the work was in progress. The worms showed the same general response as the immature forms, being positive to weak illuminations of 0.001 foot-candle, and becoming negative at about 0.01 foot-candle. A conspicuous difference between the immature and mature worms lay in the behavior of the epitokal segments as a locomotor contraction wave passed over the junction between them. In the immature worms the contraction wave passed over the entire worm almost without diminution, while in the mature forms, both male and female, the contraction wave often died before more than a few epitokal segments were passed, and the posterior end of the worm was pulled passively by the atokal portion. As the intensity was increased further, the epitokal portion suddenly began a series of prolonged, unoriented, convulsive twisting movements, originating at the posterior end. These movements continued until the epitoke became severed from the atoke or the epitoke became snarled and tangled into a knotlike, twisted mass. If part or the whole of the epitoke became separated, either it continued the uncoordinated writhing movements until it ruptured, or it became twisted and snarled, or it swam toward the light with the posterior end foremost in a series of graceful spirals. Such swimming epitokes could be made to follow a light for hours, until they became exhausted or ruptured.

Mature epitokes, when separated from the atokes, showed a response at a much lower intensity than when attached to the atokal portion. At intensities of about 0.0005 foot-candle the animals either responded by convulsive, knotlike, twisting and writhing movements or swam in spirals toward the light. The epitokes continued positive to intensities of at least 50 foot-candles. Both types of response were initiated at the posterior end and are the result of the contraction of similar muscular elements, but one was coordinated and resulted in movement of the epitoke as a whole, while the other was uncoordinated, resulting in ineffectual convulsive twisting and writhing movements. It was thought that the former behavior was found in the worms more nearly ready to swarm, for they often ruptured, shedding their sex products almost completely, while the worms exhibiting the writhing movements seldom shed sex products from more than a few scattered segments.

No difference could be determined between the atokes with and without the sexual end in regard to the threshold and response, except as the response was modified by the stimulated epitoke as described above.

LIGHT AND THE SHEDDING OF SEXUAL PRODUCTS

One of the most spectacular of the phenomena connected with the Atlantic palolo is the shedding of the sex products by the free-swimming epitokes. Mayer (1902, 1908) describes the process succinctly as follows: "When the sun is about to rise and the first faint rays of light fall over the ocean, the worms begin to contract violently, so that the sexual products are cast out through rents and tears in the dermo-muscular wall, and the torn and shrivelled cuticula sinks down to die upon the bottom." As pointed out by Mayer in the same papers, light is not a necessary factor, for free-swimming epitokes which were placed in a darkroom ruptured, but usually some hours after their fellows in sunlight.

During the night of July 2-3, 1938, an abundant swarm of the Atlantic palolo appeared over West Loggerhead Reef, beginning about 9:30 p.m. and ending at 6:09 a.m. Details of the swarm are described elsewhere (Clark and Hess, 1940) but several observations bearing on the effect of light on the bursting of the epitokes merit consideration. At dawn, the rate at which epitokes burst increased markedly until 6:09 a.m., when the last one had shed its sex products. However, the light intensity had increased almost ten thousand fold before the last one had disappeared.

During the course of the swarm many free-swimming epitokes were brought into the laboratory, the threshold intensity necessary to evoke a positive response was found, and attempts were made to determine the intensity necessary to cause bursting.

Free-swimming epitokes from the swarm orient to light, the threshold varying from 0.0005 to 0.1 foot-candle. As the intensity is increased, individuals swim in a straighter path with smaller spirals and continue to be positive up to 78 foot-candles, the maximum horizontal intensity used. Any piece of epitoke long enough to swim will orient and move toward a source of light, with the posterior end directed toward the light. However, pieces of epitoke with the posterior asexual end lacking show a higher threshold, varying from 0.001 to 0.1 foot-candle, than do complete epitokes or pieces containing the asexual posterior end.

Lamps suspended over a 10-gallon round glass aquarium were used to test the intensity of illumination necessary to cause rupture of the epitoke. The range of intensities over which the epitokes ruptured varied from less than 0.001 to 103 foot-candles, the maximum intensity which could be secured with the experimental arrangement. Often epitokes would burst as they began to orient to the horizontal beam used in testing their threshold response. Many burst at intensities of 1 to 5 foot-candles, but numbers did not rupture at intensities of over 100 foot-candles. The observations in the darkroom substantiated observations made the next morning in the field, that wide variations

in the intensity necessary to cause bursting were found in any random sample of swarming individuals.

It seemed possible that some internal factor or factors modify the response to light. Internal changes do take place, for Mayer (1908) pointed out that worms in the dark in still water eventually ruptured, but later than those which were exposed to light. The authors found that decreasing the temperature decreased the rate of the internal

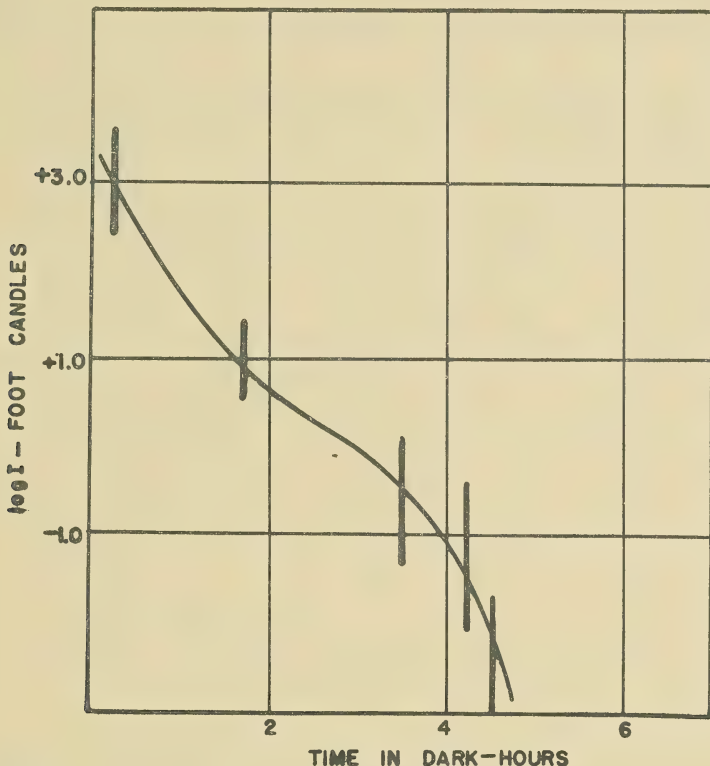


Fig. 1. Relation between length of free-living existence of epitokes in the dark and intensity of light necessary to cause rupture and shedding of the sex products. The heavy vertical lines show the range of experimentally determined intensities.

changes causing rupture and increased the length of life of the free-swimming epitoke.

To study the effect of the internal changes in the epitoke on the response to light, it was necessary to know the time of the beginning of the free-living existence of the epitoke, an observation impossible to make on epitokes secured during a general swarm. On three occasions, however, worms in rocks enclosed in floating cars swarmed, and the beginning of the free-living existence of the epitokes was determined to within 5 minutes. The epitokes were taken immediately to the darkroom and the following series of studies were made: (a) determination of the intensity necessary to cause rupture after various periods in the

dark; (b) determination of length of free-living existence when exposed to different constant intensities of continuous illumination.

Usually five epitokes were used for each point in each series. The results are given in figures 1 and 2.

It will be noted in figure 1 that the intensity necessary to cause rupture of the epitokes decreased as the length of the free-living existence increased. From an intensity of approximately 100 foot-candles after a life of 1 hour, the necessary intensity decreased to less than 0.01 foot-candle at 4.5 hours. The most probable conclusion is that

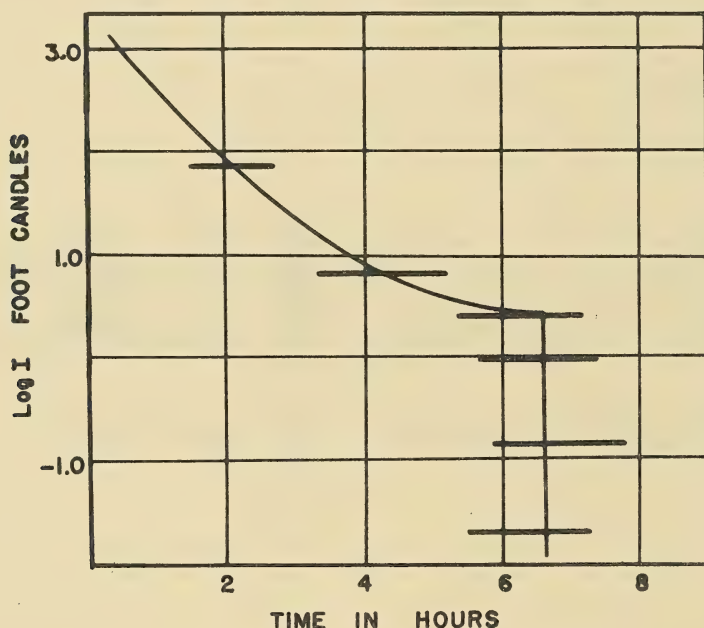


Fig. 2. Relation between length of free-living existence of epitokes and intensity of light to which they are continuously exposed. The heavy horizontal lines indicate the range of length of life at the different intensities.

changes take place in the epitoke that eventually result in its rupture. These changes result in increased sensitivity to those stimuli which contribute to, or may bring about, the shedding of the sex products, of which light is one.

Figure 2 illustrates this conclusion. Epitokes exposed to a low illumination have a longer free-living existence than those exposed to higher intensities, over 6 hours at 1 foot-candle and only 2 hours at 88 foot-candles. The shorter time before the rupture of epitokes at the same intensities in the first series of experiments is due at least in part to increased sensitivity resulting from dark adaptation in the group.

DISCUSSION AND CONCLUSIONS

Although the Atlantic palolo may swarm occasionally at other times, the greatest number of abundant swarms occur at the time of the third quarter moon. No swarms have ever been reported at the time of the new moon. This would indicate a lunar influence on swarming. The influence might be indirect through the agency of tides, etc., or direct through the action of moonlight itself. Mayer (1908) and Clark and Hess (1940) present various observations eliminating tidal action as a possible factor.

Moonlight reaches a maximum intensity of 0.02 foot-candle at the full moon and about 0.002 foot-candle at the quarter moon (Smithsonian Meteorological Tables, 1918).

Immature worms are positive to intensities varying from 0.001 to 0.01 foot-candle, after which they become negative. This means that the immature worms are confined to their burrows by their negative response during the day and at night when moonlight intensity reaches approximately 0.01 foot-candle. Conversely, this means that they will emerge from their burrows to feed only during certain parts of the night. The length of the feeding period will be determined by the intensity and duration of the moonlight, both of which are determined by the lunar cycle. The atokal portion of mature worms has approximately the same threshold for response and it, too, shows a periodicity in feeding related to the lunar cycle. Such a mechanism may be important as a means of forcing the sexual development of the worms into step with the lunar cycle, resulting in maturity and swarming at a definite phase of the moon.

The response of the epitoke does not appear to add new information regarding the factors involved at the moment of swarming.

The positive orientation to light of the free-swimming epitokes causes them to swim to the surface, where light is most intense. From the inauguration of their free-swimming existence until they rupture, the epitokes become progressively more sensitive to light which induces rupture. Coincident with the increase of sensitivity is the rapid increase of light intensity at dawn. The result is an almost simultaneous rupturing of the remaining epitokes, assuring a very efficient mass shedding and fertilization of eggs. The efficiency of the mechanism is demonstrated by the short duration of even a major swarm after dawn (Clark and Hess, 1940).

SUMMARY

1. Immature worms and the atokal portion of sexually mature worms are positive to light intensities from about 0.001 to 0.01 foot-candle. As the intensity increases they become negative.

2. Moonlight reaches a maximum intensity of 0.02 foot-candle at the full moon and about 0.002 foot-candle at the quarter moons.

3. Thus moonlight covers a range of intensities adequate to change the positive response of the worms to a negative response, so that they are confined to their burrows at night at certain periods of the lunar cycle. It is suggested that this may be one of the contributing factors causing sexual development to concur with the lunar cycle and major swarming to occur at definite quarter moon phases.

4. Free-swimming epitokes are positive to all intensities of light used above the threshold of about 0.005 to 0.1 foot-candle.

5. Variations in the intensity of light necessary to cause epitokes to rupture and shed their sex products are due to increase in sensitivity to such light with increase in length of the free-living existence of the epitokes.

6. The efficiency of the responses of the epitoke in assuring mass fertilization is pointed out.

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IV

CYTOLOGICAL STUDIES ON THE STRUCTURE AND DIVISION
OF THREE NEW CILIATES FROM THE LITTORAL
EARTHWORM OF TORTUGAS

By RALPH WICHTERMAN

Temple University

With twenty figures

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CYTOLOGICAL STUDIES ON THE STRUCTURE AND DIVISION OF THREE NEW CILIATES FROM THE LITTORAL EARTHWORM OF TORTUGAS

INTRODUCTION

At the Tortugas Laboratory during the summer of 1939 (Wichterman, 1939), a study was begun of the protozoa that were found inhabiting the intestine of the littoral earthworm *Pontodrilus bermudensis* Beddard. The investigation revealed the presence of three hitherto undescribed ciliates: *Hystero-cineta pontodrila*, n. sp.; *Anoplophrya macronucleata*, n. sp.; and *Maupasella leptas*, n. sp. The primary purpose of this paper is to describe the ciliates and give an account of fission in each species.

The investigation was continued at the Marine Biological Laboratory, Woods Hole, Massachusetts, and at Temple University.

The author wishes to record his indebtedness to the Carnegie Institution of Washington for making this study at the Tortugas Laboratory possible, and especially to the late Professor David H. Tennent, Executive Officer of the Laboratory, for his kindly assistance. Credit is also given to the Biological Institute, Philadelphia, Pennsylvania, for aid given throughout the work.

MATERIALS AND METHODS

Materials. All three species were found living in the intestine of *Pontodrilus bermudensis* Beddard, a remarkable marine earthworm of the intertidal zone of Loggerhead Key, Tortugas, Florida. The worms, which were very abundant, were found under partly covered windrows of decomposing eelgrass (*Cymodocea manatorum*) and turtle grass (*Thalassia testudinum*) from about 2 to 15 cm. beneath the surface of the wet sand and at times very close to the water's edge. Such vegetation was thrown on the beach by the incoming tide and generally buried under a layer of sand. The worms clustered about this decaying organic matter, which served as food.

Abundant material may be easily obtained by digging the worms from among this moist and decaying seaweed. Gowanlock (1930), who made an ecological and physiological study of this worm, also reported that they were abundant and that their distribution in nature is directly controlled by the distribution of windrows of *Sargassum*, which he believed constituted the entire food of this littoral oligochaete. There were fewer worms on the west-northwest side of the island near the boat dock than on the opposite side. This may be due to the fact that less vegetation is thrown up on that shore.

Beginning on June 19, 1939, collections of worms were made daily from various parts of the island. The last collection was made on July 24, 1939.

The collected worms, with a small amount of the wet sand in which they were found, were brought into the laboratory and immediately examined for intestinal ciliates.

Methods. Observations were made both on living forms and on fixed and stained specimens.

To obtain ciliates for study, the worms were washed free of sand with fresh clean sea water. For dissection, it was found most desirable to cut the worm into three sections, then to pin each section down to a piece of cork and slit the body wall. The intestine was then removed and teased apart, the ciliates being thus liberated for study in a small amount of filtered sea water. This appeared to be a favorable medium in which to study the living ciliates.

For the permanent preparations, thin smears of intestinal contents were made on cover slips. Killing and fixing agents used were Bouin's and Schaudinn's fluids. Schaudinn's fluid was heated to 45° C., after adding 5 per cent of glacial acetic acid.

Mayer's haemalum, with occasional use of eosin as a counterstain, and Heidenhain's iron haematoxylin were the stains used, and gave very satisfactory results. With Heidenhain's method, finer differentiation was obtained by using Tuan's (1930) modification, namely, destaining with a saturated aqueous solution of picric acid, then washing in ammonia water.

After fixation and washing, most of the smears were carefully packed in vials of a diameter slightly larger than that of the circular cover slips. The cover slips were prevented from touching or rubbing by the use of circular paper separators, after the method of Chen (1937). Such smeared cover slips were removed from the preservative (70 per cent alcohol) in the laboratory in Philadelphia and subsequently stained.

INCIDENCE OF INFECTION

Two hundred and thirty worms were dissected and examined. Of that number, 64 per cent were infected with the new ciliates. *Hysterozineta pontodrila* was found in 52 per cent of the worms examined, *Anoplophrya macronucleata* in 30 per cent, and *Maupasella leptas* in only 4 per cent. When *Hysterozineta* or *Anoplophrya* was present, the infection as a rule was quite heavy. Generally a worm was parasitized with two different species, but *Hysterozineta* was found exclusively in 30.4 per cent of those examined, *Anoplophrya* in 9.1 per cent, and *Maupasella* in 0.44 per cent. Approximately 0.87 per cent of the worms contained all three ciliates; 18.7 per cent contained *Hysterozineta* and *Anoplophrya*; 1.3 per cent contained *Hysterozineta* and *Maupasella*; and 1.3 per cent contained *Anoplophrya* and *Maupasella*. Infection with *Maupasella* was very light.

Generally the middle part of the intestine was the principal seat of infection for *Anoplophrya*, and the posterior region contained mainly *Hysterozineta*. Beers (1938), working with intestinal ciliates of *Eisenia lönnbergi*, also found a regional specificity of ciliates for certain parts of the intestine. It is interesting to note that he observed a species of *Hysterozineta* which occupies a posterior region of the worm. On the other hand, Conklin (1930) recorded that specimens of *Anoplophrya marylandensis* were found only in the anterior third of the intestine and were most numerous immediately posterior to the gizzard in the earthworms *Lumbricus terrestris* and *Helodrilus caliginosus*.

HYSTEROZINETA PONTODRILA, n. sp.

(Figures 3 to 9)

General Structure

For a historical review of the genus *Hysterozineta* and a table of comparative data on the known species, see Beers (1938). *Hysterozineta pontodrila* is the fifth species of the genus to be described to date. The ciliate is dorsoventrally flattened, with the dorsal surface slightly convex and the ventral surface concave. The anterior end tapers to a blunt point, and the posterior end widens to become truncate. Viewed from the dorsal or ventral (fig. 3) surface, the organism is somewhat pyriform in outline.

Average dimensions of 50 fixed organisms taken at random: Length, 121 microns (range, 87.3-157.5); width, 53 microns (range, 38.7-70.2).

Behavior. The body is very flexible, and is only 29 microns thick. Living animals swim rather rapidly for a time, then attach themselves by their anterior ends to some host material. The anterior end is very thigmotactic. When swimming freely, the body assumes a concave shape ventrally, and convex dorsally (fig. 4). In dorsal view, the ciliate appears curved or bent, the longer side of the body being on the left and the shorter arc on the right.

Characteristic of the genus *Hysterozineta* is the posteriorly located mouth and associated ingestatory structures. On the left posterior margin of the body there is a deep tubular invagination, the cytopharynx, about 18 microns long and 3 microns wide, which appears to lead directly into the cytoplasm (fig. 5). The opening of the slit is wide, and the extreme posterior part of the body forms a thin but narrow platform. A short distance from this platform there is a row of close, stiff, curved cilia. These cilia form a continuous band about 30 microns long, starting at a region near the ingestatory canal and extending about halfway around the posterior

end. Cilia were not detected in the ingestatory canal. Cytoplasmic inclusions resembling food vacuoles may be found in the posterior region of the body only (figs. 3, 6). Active cyclosis in the body proper is absent.

Special structures. The characteristically inverted V-shaped sucker is found anteroventrad. The two "pads" which make up the sucker are not of the same size, the left pad being conspicuously shorter and slightly thicker than the right one. Measurements of a typical animal show the left pad to be 34 microns long by 16 wide, and the right pad 41 microns long by 14 wide. Though the pads themselves are devoid of cilia, long cilia, measuring about 7 microns, which beat posteriorly are found in the wedge-shaped depression between them. A definite fibrillar pattern (fig. 3) is noticeable in and below the pads of living as well as fixed and stained specimens.

Vacuoles. The presence of vacuoles in the posterior part of the body, strongly suggesting food vacuoles, is worthy of mention (see figs. 3, 6). Nutrition appears to be mainly saprozoic, occasionally holozoic. Powdered carmine and Chinese ink were placed in the medium surrounding many specimens, yet after 2 hours no ingestion of these substances occurred; nor has ingestion of any organic material ever been observed.

In the right posterior part of the body, a few to many small contractile vacuoles are present, which may coalesce and empty to the outside. There appears to be generally one larger or main vacuole into which the smaller ones empty. When this larger one contracts, it becomes smaller but does not entirely disappear from view. Contractile vacuoles are not generally spherical; an average large one measured 20 by 14 microns and took about 4 seconds to empty. Approximately 2 minutes pass between contractions of the vacuole. There may be as many as 5 smaller vacuoles operating independently and contracting at different times, but they are usually found in the same region of the body.

Nuclei. A conspicuous macronucleus and micronucleus can be seen easily in the living animal.

The macronucleus is very long, centrally located, and parallel to the long axis of the body, measuring 62 by 10 microns (average of 50 specimens). It is somewhat cylindrical in shape, with tapering blunt ends, and is generally slightly constricted in the center. It is heavily granular, with very coarse as well as finer chromatin granules.

Always on the left side of the center of the macronucleus and lying near its constriction is the oval micronucleus, which measures 4 by 3 microns. This body stains readily with nuclear dyes, and in the interphase stage appears as a clear homogeneous body surrounded by a nuclear membrane.

Division

The abundant material showing fission permitted a detailed study of the process. Cytosomal division at the beginning appears markedly unequal, the anterior daughter being much larger than the posterior one (fig. 7). Toward the end of the process, however, division appears to be equalized (fig. 9). The first indication of division appears in the micronucleus, which divides mitotically. During interphase the micronucleus takes the nuclear stain intensely (fig. 3), but in early fission the deep stainability is lost as chromosomes are being formed. Soon after the first visible change in the micronucleus, a constriction is noted in the body, usually well below its mid-region. The constriction is first noted on the side of the body where the micronucleus is located (fig. 6). Although great numbers of mitotic stages were examined, the chromosome number could not be determined, owing to their large number, small size, and refractivity to stain. Nevertheless, well defined prophase, metaphase, anaphase, and telophase stages were observed (figs. 6, 7, 8). Along with increased mitotic activity, further constriction of the body occurs. It is only near the very end of the micronuclear division that the first constriction of the macronucleus occurs for its amitotic division (fig. 8).

As division proceeds there is a general dedifferentiation of specialized structures, a phenomenon which is characteristic of most ciliates having such structures. The sucker, though never lost from view, is less conspicuous. The cytopharynx at the posterior region becomes completely dedifferentiated and is lost from view. A newly differentiated cytopharynx makes its appearance as a tubular structure in the posterior region of the dividing animal on the side opposite the micronucleus (fig. 6). Later a somewhat similar tubular structure arises *de novo* in the anterior daughter (figs. 7, 8, 9). Both new cytopharyngeal structures then shift their positions gradually toward the side opposite where they were originally, and eventually they are found on the same side with the micronucleus. The contractile vacuoles of the parent are retained by the posterior daughter, and the anterior daughter forms a new set. A new sucker appears in the posterior daughter (fig. 9), and the anterior sucker is retained by the anterior daughter after undergoing some reorganization.

Toward the end of division, the two daughters resemble each other very closely in size and shape. Finally the two break apart and each grows into a typical vegetative individual.

ANOPILOPHRYA MACRONUCLEATA, n. sp.

(Figures 1, 2, 10 to 15)

General Structure

Size and shape. *Anoplophrya macronucleata* is an astomatous ciliate measuring (average of 50 specimens) 101 microns in length (range, 70.2-148.5) and 69 in width (range, 52.2-85.5). See figure 10, and for side view figure 11.

The body of the ciliate is broadly pyriform, with the anterior end blunt and the posterior end pointed. A thin but definite ectoplasmic region about 2 microns thick is present beneath the pellicle. This region is thickest at the broad anterior end. The body is completely covered with cilia. Ciliary lines on the pellicle are closely set, being approximately 0.7 micron apart. Emanating from them are the cilia, which measure about 6 microns in length. Specialized structures such as a mouth, attaching organ, or spine are absent.

Behavior. The ciliate moves about actively in a spiral fashion, and reminds one of *Balantidium* as it burrows through debris. Occasionally bits of debris cling to the posterior end.

Contractile vacuoles. The contractile vacuoles are generally numerous. In 32 specimens observed at random, the average number was about 8 (range, 4-11). It appears that the larger the ciliate, the greater the number of vacuoles. Their largest diameter before contraction is about 7 microns; after contraction, about 1.2 microns. They are never lost from view. The interval from one contraction of a given vacuole to the next is about 5½ minutes, but the emptying of a vacuole takes about a second.

Nuclei. The macronucleus, which is centrally located in this ciliate, is massive in appearance. In 50 measured specimens, the average length was 56 microns (range, 31.5-97.2), and the average width 21 microns (range, 11.7-29.7). The shape is roughly triangular, the anterior end being very broad. The outer surface of the macronucleus is rough with many sharply pointed surfaces. Outlines of 20 drawings of the macronuclei (fig. 1) show the variations in shape and size of this body. There is a direct relation between macronuclear size and the size of the ciliate; the larger the animal, the larger the macronucleus (fig. 2).

The macronucleus is coarsely granular and takes nuclear stains readily. At times the coarse granules appear to be in a matrix of fine, uniformly smaller granules. A "pocketed" condition of the macronucleus similar to that described for *Paramecium trichium* by Wenrich (1926) was occasionally seen in late division stages (figs. 13, 14, 15). Although hundreds of well stained specimens were carefully examined for the presence of micronuclei,

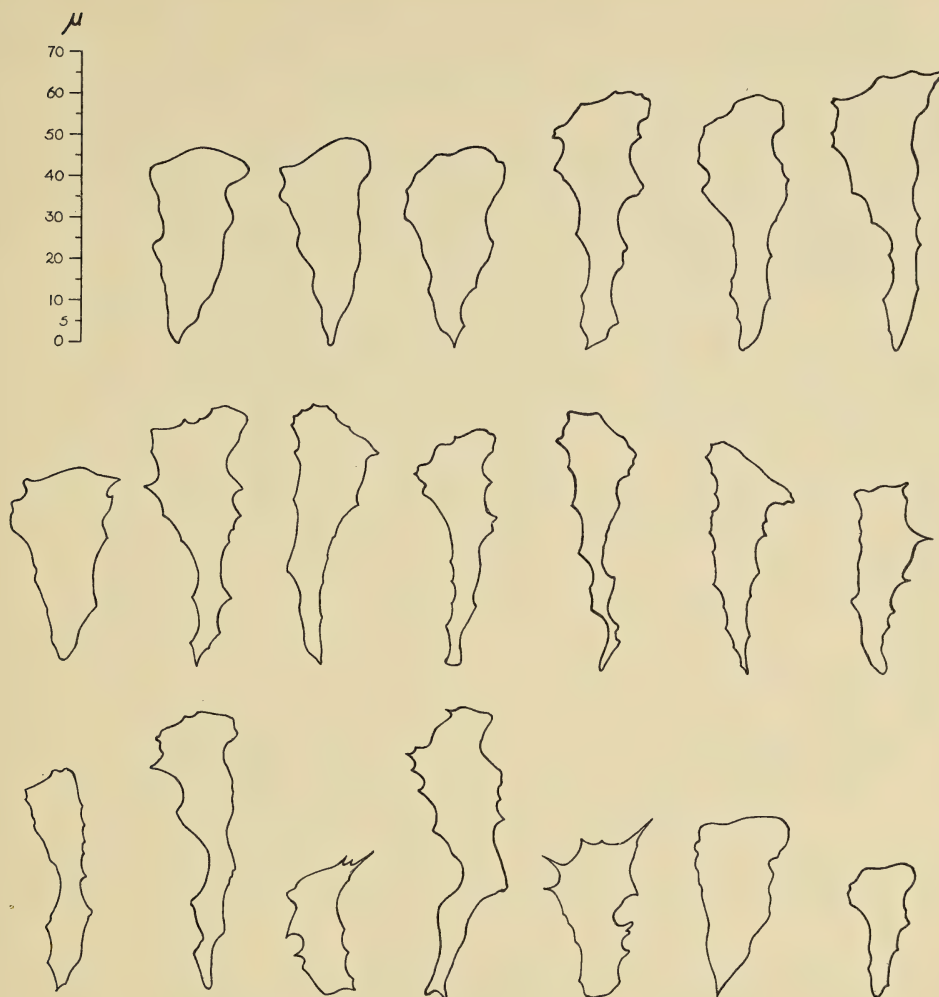


Fig. 1. Variation in size and shape of 20 macronuclei of fixed and stained specimens of *Anoplophrya macronucleata*, selected at random and drawn with aid of camera lucida.

such structures could not be identified with certainty. It would be easy for a small micronucleus to remain hidden in a cavity of the irregularly shaped macronucleus. On the other hand, if a micronucleus were present, one would expect to see mitotic stages during division.

Division

The first indication of division in *Anoplophrya macronucleata* is a lengthening out of the macronucleus and the appearance of a constriction in the center of the ciliate (fig. 12). Later in the dividing process the prospective anterior daughter appears wider and longer than the posterior daughter, but toward the end of the process the division, as noted above,

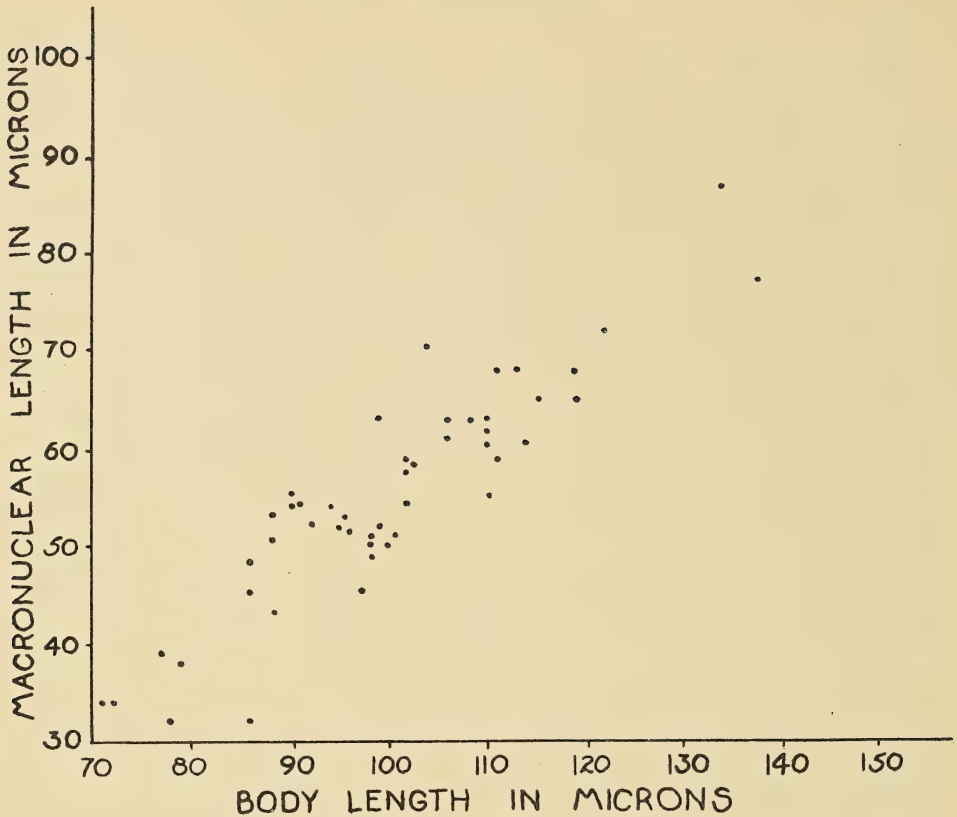


Fig. 2. Relation between length of macronucleus and length of body in 50 fixed and stained specimens of *Anoplophrya macronucleata*.

takes on the appearance of an equal one (figs. 13, 14). During division, the contractile vacuoles are generally uniformly distributed, one half going to each daughter individual.

After fission is well under way, a change is seen to occur in the structure of the macronucleus, and a quantity of residual macronuclear chromatin is cast into the cytoplasm, where it is absorbed (figs. 13, 14, 15). This phenomenon has been extensively reported for holotrichous ciliates by Kidder and his associates (Kidder and Claff, 1938).

MAUPASELLA LEPTAS, n. sp.

(Figures 16 and 17)

General Structure

The genus *Maupasella* was created by Cépède (1910) for the single species *M. nova*, in which he described two distinct forms. One form was stocky and measured 82 microns in length including the fixing organ; the greatest width was toward the anterior part of the body, which measured 39 microns;

the astome tapered gradually toward the posterior end of the body. The long forms measured 117 microns in length and 18 microns at their greatest width; in these forms, the tapering toward the posterior end of the body was very slight.

Measurements of only 9 specimens of *M. leptas* show the average length to be 72 microns (range, 45-94) and the average width 25 microns (range, 18-32).

The ciliate is gracefully slender in shape (fig. 16). When seen from the side, one surface is concave and the other is convex. The anterior end terminates in a sharp spine, and the posterior end is blunt.

Ciliary lines are prominent; about 40 to 50 are found around the body, parallel to its long axis. The cilia measure about 6 microns in length except at the posterior end, where they are much longer. At the extreme anterior tip of the protozoon and projecting off to one side is the sharply pointed spinous fixing cell organ, measuring 6 microns in length.

Contractile vacuoles. The contractile vacuoles are 3 to 4 in number. One or two may be located in the center of the body and the remainder may be placed posteriorly. Drawings by Cépède of *M. nova* show from 3 to 12 contractile vacuoles.

Nuclei. The macronucleus is extremely large and in the center of the organism, with its long axis parallel to that of the body. It is generally cylindrical in shape, measuring about 44 microns in length by 6 in width. The macronuclei of the short forms of *M. nova*, according to Cépède, measure 69 by 5 microns; those of the long forms, 105 by 3 microns.

The micronucleus of *M. leptas* is a small oval body measuring approximately 2 by 3 microns. It is located near the center of the macronucleus and to one side of it.

Division

Division of *Maupasella leptas* appears to be not unlike that of other closely related species, so that little space will be devoted to description of the process (fig. 17). The anterior daughter retains the old spinous attaching structure, and the posterior daughter forms another one *de novo*.

PRESENCE OF OTHER PARASITES

Acephaline gregarines (figs. 18-20). Though the investigation was directly concerned with the intestinal ciliates, some observations were made on stages in the life cycle of acephaline gregarines found in the intestine and seminal vesicles of the worm.

Trophozoites, as seen in the living condition, are deeply granular and brown in color, are smooth, and measure 36 by 110 microns (fig. 18). Peristaltic contractions run along their entire length. The nucleus is not visible in the living organism.

The early gametocyst as seen in the living condition measures 176 by 248 microns (fig. 19). Nuclei are visible in the deeply granular and dark gametocytes. Mature gametocysts measure 136 by 260 microns and are tightly packed with spores measuring 11 by 20 microns (fig. 20).

Nematodes. Young nematodes were found in 33 per cent of the 230 worms examined. Much larger nematodes, which might have been adult stages of the young found in the worms, were present in great numbers in the wet sand near the earthworms.

DISCUSSION AND CONCLUSIONS

For a detailed study of the taxonomy of astomatous ciliates, reference may be made to the excellent papers of Cheissin (1930) and Heidenreich (1935). It seems noteworthy that representatives of three genera of holotrichous ciliates are found in this marine earthworm, two of which are definitely astomatous and one, *Hysterozineta*, has ingestory structures which may be in the process of evolution toward the astomatous condition.

Neither encystment, conjugation, nor stages of nuclear division resembling autogamy or endomixis were observed in feces or in dissected worms. In an attempt to discover the life cycle of the ciliates, 10 worms were washed in filtered sea water and placed with some vegetation on wet filter paper in Petri dishes. Fecal material was examined periodically for the next 72 hours, but cysts or other stages could not be found. On the other hand, nematode eggs were passed out by the worms in large numbers.

The method of transmission of ciliates from one worm to another therefore remains to be discovered. Some simple experiments were made in an effort to throw light on this question. Infected worms were washed in filtered sea water and dissected. Then the ciliates were removed with a capillary pipette and placed in freshly filtered sea water. Twenty-three specimens of *Hysterozineta* when first placed in the water appeared to behave normally. Individuals were seen to swim about actively for about 3 hours, slow down, then die; a few, however, were found alive 6 hours after being placed in the water. Thirty-six specimens of *Anoplophrya* were similarly placed in sea water, where they appeared normal and active for about 3 hours. After that time, vacuolation gradually occurred, and the animals moved slowly, then died. A few, however, remained alive for nearly 8 hours. The comparatively small number of specimens of *Maupasella* encountered in the study precluded experimentation.

The absence of cysts from the feces and the apparent longevity of ciliates in sea water suggest that the infestation may be spread from one host to another directly without the formation of cysts. When a worm dies and decomposes, some ciliates undoubtedly remain alive in the decomposing body in

the wet sand. Such ciliates may readily be ingested with vegetation by other worms. If the ciliates are able to withstand the digestive action of the host worm, direct infection without the necessity of cysts may occur.

Gowanlock (1930) reports: "The experimental studies clearly established that this species of earthworm possesses remarkable physiological attributes involving a high degree of adaptation to sea-beach life. . . . This earthworm was found to survive apparently unaffected temporary immersion in the sea to a depth of over 500 meters, exposure among the coral reefs for 22 days and submergence in shallow sea-water for the entire period of 74 days available for these experiments. Its survival in conditions of lowered oxygen pressure induced by various methods demonstrated an astonishing resistance to a practically anaerobic environment." It would be of some interest to know the fate of the intestinal protozoa of such immersed worms.

Gowanlock also recorded the role played by the sooty tern, *Sterna fuliginosa* Gmelin, and the noddy tern, *Anous stolidus* Linn., as vectors of the worm from island to island. Examinations for intestinal protozoa of worms not only from the keys making up the Dry Tortugas group, but from the Bahamas and West Indies as well, might throw considerable light on host-parasite relations.

SUMMARY

1. Three new holotrichous ciliates are described that were found inhabiting the intestine of *Pontodrilus bermudensis* Beddard, a remarkable marine earthworm of the intertidal zone of Loggerhead Key, Dry Tortugas, Florida. These ciliates are *Hysterozineta pontodrila*, n. sp., *Anoplophrya macronucleata*, n. sp., and *Maupasella leptas*, n. sp.

2. Division in all three species has been described and discussed. During the division of *Anoplophrya macronucleata*, elimination of macronuclear chromatin occurs.

3. Of 230 worms examined, 64 per cent were infected with the ciliates. *Hysterozineta pontodrila* was found in 52 per cent, *Anoplophrya macronucleata* in 30 per cent, and *Maupasella leptas* in 4 per cent. Generally a worm was parasitized with two different species, but *Hysterozineta* was found exclusively in 30.4 per cent, *Anoplophrya* in 9.1 per cent, and *Maupasella* in 0.44 per cent.

4. Observations on the length of life of ciliates in sea water are recorded.

5. Encystment or conjugation has not been encountered, but a method of transmission from one worm to another is suggested.

6. The presence of stages in the life cycle of acephaline gregarines and nematodes was noted.

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FIGURES 3 TO 20

All drawings were made with the aid of a camera lucida from fixed and stained preparations, except where indicated. Fixatives used:¹ Schaudinn's fluid and Bouin's fluid. Stains used: Heidenhain's haematoxylin and Mayer's haemalum with occasional use of eosin as a counterstain. In printing, the drawings have been reduced one-half.

FIGURES 3 TO 9

Hysterozineta pontodrila, n. sp.

Fig. 3. Ventral view of typical vegetative ciliate, showing inverted V-shaped sucker at anterior end, with fibrils; also showing cilia, macronucleus, contractile vacuoles. Food vacuoles near posteriorly located cytopharynx. X 450.

Fig. 4. Lateral view, showing thinness of body. Note tapering anterior end of macronucleus and lack of cilia on sucker. X 175.

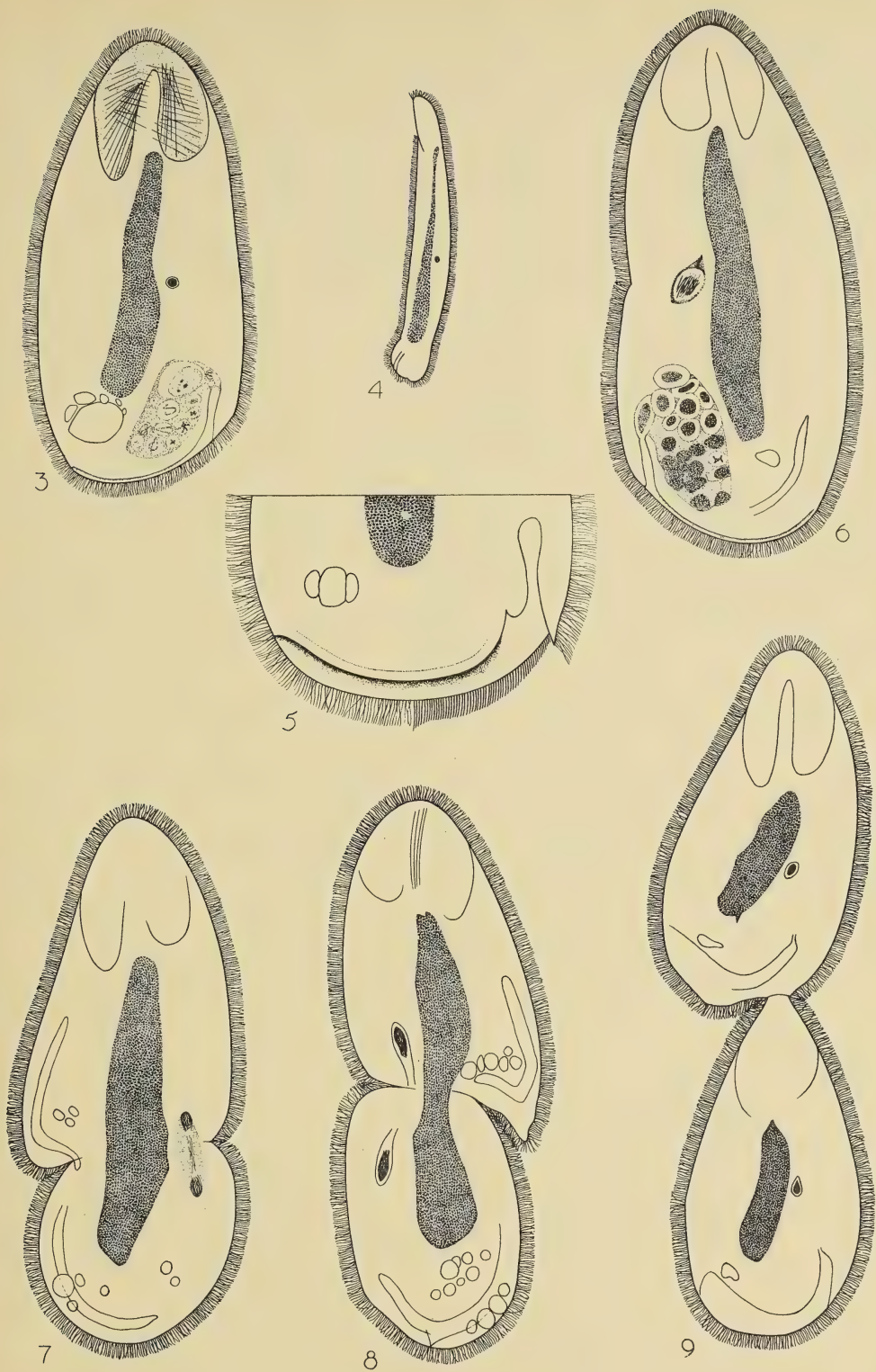
Fig. 5. Free-hand sketch of posterior end of living specimen, showing detail of platform below cytopharynx. Observe stiff cilia on posterior edge of ciliate near cytopharynx. X 875.

Fig. 6. Division, early stage, dorsal view. First evidence of constriction on left side of body; micronucleus in metaphase stage (note chromosomes). Food vacuoles and inclusions near old cytopharynx while new cytopharynx is being formed. X 450.

Fig. 7. Division, ventral view. Micronucleus in anaphase stage. Constriction of body clearly visible. Old cytopharynx completely redifferentiated; two new cytopharyngeal structures are shown. X 450.

Fig. 8. Division, dorsal view. Micronucleus in late telophase stage and macronucleus preparing to divide amitotically. Constriction of body conspicuous at this stage. X 450.

Fig. 9. Division, ventral view. Micronuclear and macronuclear division completed. Newly differentiated cytopharyngeal structures shifting to usual positions on opposite side of ciliate. Note new sucker being formed in posterior daughter individual. Final stage prior to separation into two daughter cells. X 450.



FIGURES 3 TO 9

FIGURES 10 TO 15

Anoplophrya macronucleata, n. sp.

Fig. 10. View of vegetative individual, showing pyriform body, cilia, and thick, clear ectoplasmic band at anterior end; also showing massive macronucleus and contractile vacuoles. X 550.

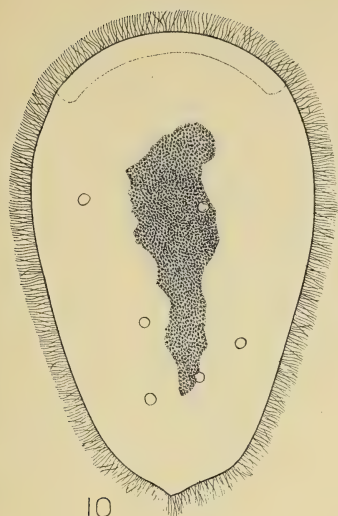
Fig. 11. Lateral view, showing shape of body and macronucleus. Contractile vacuoles always visible close to one surface of the pellicle. X 235.

Fig. 12. Division, early stage. Note constriction of macronucleus and body. X 550.

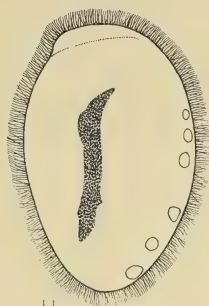
Fig. 13. Division, later stage. Constriction of macronucleus and body well advanced. Note "pocketed" condition of macronucleus, and chromatin in cytoplasm. X 550.

Fig. 14. Division, very late stage. Amitotic macronuclear division completed, with chromatin in cytoplasm. X 550.

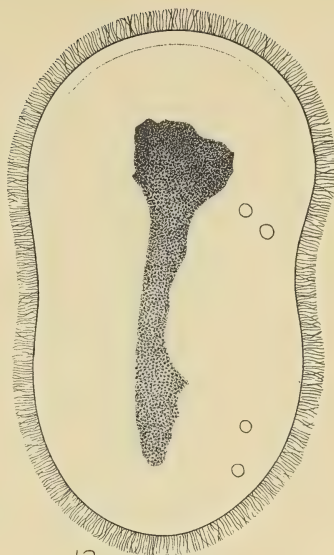
Fig. 15. Anterior daughter of recently divided individual, showing "pocketed" condition of macronucleus, and extruded macronuclear chromatin in cytoplasm. X 550.



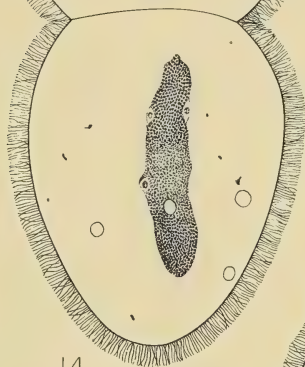
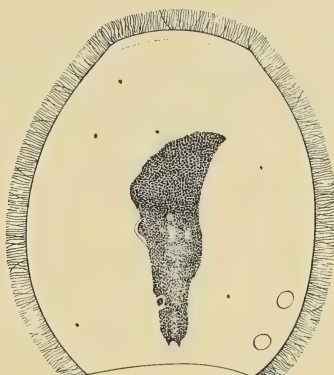
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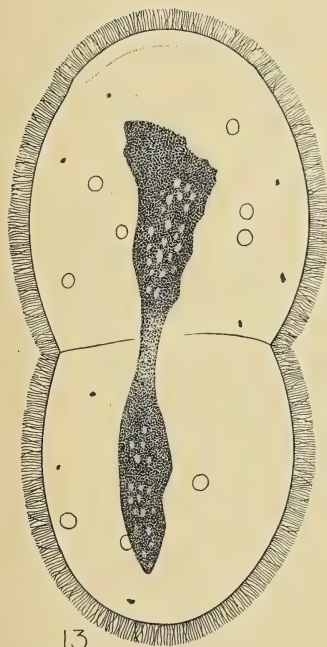
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FIGURES 10 TO 15

FIGURES 16 TO 20

Maupasella leptas, n. sp.

Fig. 16. Vegetative individual, showing slender, ellipsoidal shape, cilia (which are longer at posterior end), spinous attaching structure, macronucleus, micronucleus, and contractile vacuoles. X 850.

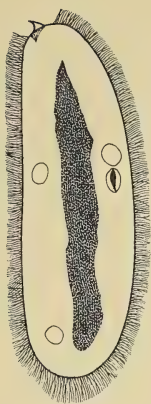
Fig. 17. Division, late stage. Note dividing macronucleus and micronucleus, the latter surrounded by a nuclear membrane. X 850.

Acephaline gregarine stages

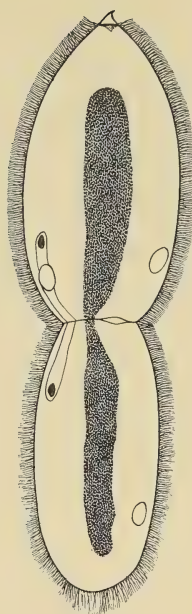
Fig. 18. Trophozoite, living; free-hand sketch. Deeply granular and brown (masking nucleus). X 250.

Fig. 19. Early gametocyst, living; free-hand sketch. Deeply granular and dark, but nucleus visible in each gametocyte. X 250.

Fig. 20. Mature gametocyst, living. Tightly packed with spores containing sporozoites. X 250.



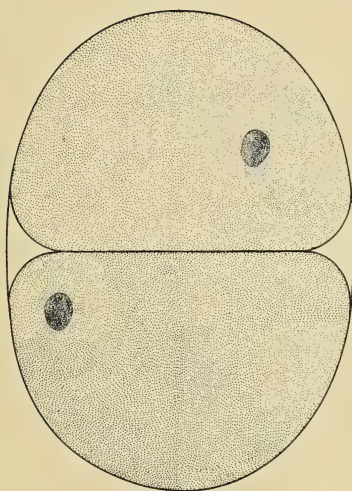
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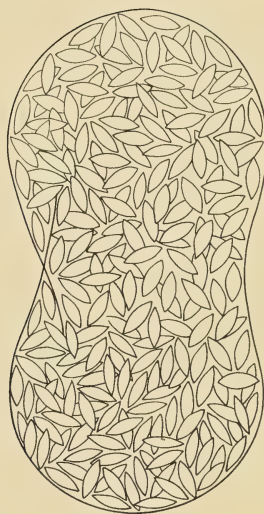
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FIGURES 16 TO 20

V

A NEW CILIATE FROM A CORAL OF TORTUGAS
AND ITS SYMBIOTIC ZOOXANTHELLAE

By RALPH WICHTERMAN
Temple University

With four figures

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A NEW CILIATE FROM A CORAL OF TORTUGAS AND ITS SYMBIOTIC ZOOXANTHELLAE

INTRODUCTION

A ciliate found on the coral *Eunicea crassa* E. and H.¹ is here described under the name *Paraeuplotes tortugensis*, n. gen. and n. sp., and is placed in the family Paraeuplotidae, n. fam. This species of coral is one of the very common members of the Alcyonaria fauna found throughout the Caribbean region, and occurs abundantly on the reefs about Tortugas, Florida (Hargitt and Rogers, 1900; Cary, 1917). The corals were found attached to "coral rock" and kept in large "live cars" that were held fast to the west dock of Loggerhead Key, Tortugas. Openings in the live cars permitted free circulation of sea water.

Organisms crawling slowly on the surface of the coral were observed in abundance by Dr. Leonard B. Clark, of Union College, who brought them to the attention of the writer. Subsequent study showed the organism to be a hitherto undescribed ciliate (Wichterman, 1940).

METHOD

A piece of the coral was placed in a finger bowl containing seawater and examined under the low-power binocular microscope. With a capillary pipette, the ciliates were removed and placed on a cover slip (24 by 50 mm.) of a specially prepared slide for microscopical study (fig. 1). Another



Fig. 1. Diagram of special slide used for studying the dorsal and ventral aspects of *Paraeuplotes tortugensis*. The glass supporting rods are 800 microns in diameter, 2.5 cm. long, and fastened to the slide 40 mm. apart.

cover slip of the same size was placed over the protozoa and the two covers were then sealed with vaseline and placed upon the parallel glass rods of the slide. This method of study proved very helpful, because the ciliates when placed on the glass cover slip quickly settled on their ventral surfaces, and tightly packed zooxanthellae made detailed study of that surface

¹The writer wishes to express his appreciation to Dr. L. R. Cary, of Princeton University, for correct identification of the coral. It is worthy of note that he recalled having seen ciliates in some numbers on various of the Alcyonaria in his work on corals.

difficult. With this special slide, both surfaces of the same ciliate could be studied in detail under the oil immersion lens by reversing the position of the joined cover slips on the slide.

MORPHOLOGY OF *PARAEUPLOTES TORTUGENSIS*, n. gen. and n. sp.

Paraeuplotes tortugensis is a hypotrichous ciliate, living individuals measuring on the average 85 microns in length by 75 in width. In outline, it is elliptical with broadly rounded ends; occasionally it is nearly circular (figs. 2, 3, 4). Observed laterally, it appears highly convex dorsally and only slightly concave ventrally.

Cilia are completely lacking from the dorsal surface (fig. 2), but on the ventral surface (fig. 3) there is a discontinuous circle of cilia which may enable the organism to adhere to surfaces. An arc of long, tightly packed cilia is anteriorly placed, and directly posterior to it are two tufts of long cilia. On the side opposite the peristome is a curved ciliary plate measuring 37 microns in length. Emanating from this structure are very long cilia, which with the region of anterior cilia make a more or less continuous ring (fig. 3). Near the extreme posterior end and to the right side is found a cluster of 5 or 6 stiff spines or cirri approximately 13 microns in length.

The adoral zone of membranelles is conspicuously well developed, beginning at the right side and extending entirely around the frontal margin, then gradually entering the sunken peristome, which runs fairly close to the posterior end of the body at the ciliary plate.

A single vacuole is found in the posterior region near the cirri. When expanded, it measures approximately 12 microns.

The large, bandlike macronucleus (fig. 4) which is so characteristic of the Euplotidae is very conspicuous, but the micronucleus is not clearly differentiated.

Fibrils (fig. 4) radiate from a point anteriad and pass to the ciliary plate and marginal wall of the peristomial membranelles.

All the many specimens observed were closely packed with the yellowish-brown subspherical unicellular alga *Zooxanthella*, measuring about 12 microns in diameter.

SIGNIFICANCE OF THE PRESENCE OF ZOOXANTHELLAE

W. L. and M. M. Doyle (1940), who have made an intensive study of the morphology and physiology of this alga, state that zooxanthellae contain "a plastid of reticulate structure having embedded in it a colorless pyrenoid surrounded by an amyloid (starch) layer, additional amyloid (starch) grains

containing no pyrenoid, an 'assimilation product,' oil droplets, red pigment granules, crystals of calcium oxalate, and the regularly occurring nucleus, cell wall, and hyaline cytoplasm."

The association between protozoa and zooxanthellae is widespread in nature, as is shown in the work of Buchner (1930). Zooxanthellae, in addition to being present in protozoa, are found in Porifera, Coelenterata, Ctenophora, Turbellaria, Rotifera, Gastropoda, and Lamellibranchia.

What is the nature of the symbiosis between the protozoon and the zooxanthellae it contains? Unfortunately, the ciliates were discovered too late in the season at Tortugas to permit experimental work, but much has been done by others on the physiology of symbiosis of unicellular algae and animals (Brandt, 1883; Pringsheim, 1928; Yonge, 1931, 1934, 1935; W. L. and M. M. Doyle, 1940). As pointed out by Yonge (1934), the zooxanthellae, in addition to gaining protection (if they are not digested), make use of the end products of animal metabolism, notably carbon dioxide, nitrogen, and phosphorus. The host, on the other hand, in the presence of light continually receives oxygen given off by the algae. Also fats and carbohydrates may pass from the algae to the host to be utilized as food. Pringsheim (1928) has shown in *Paramecium bursaria* that organic matter may be passed from unicellular green algae (*Zoochlorella*) to the protoplasm of the ciliate, where it must unquestionably be used for food.

The hypotrichous ciliates which were studied were free of organic food material other than zooxanthellae (some of which were in various stages of division), and the writer is therefore inclined to believe that the ciliates live by utilizing the products of holophytic nutrition of these symbiotic organisms.

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FIGURES 2 TO 4

All figures are of *Paraeuplotes tortugensis*, n. gen. and n. sp., as observed under the oil immersion lens, and were made with the aid of a camera lucida. Magnification, $\times 750$. In printing, the drawings have been reduced one-half.

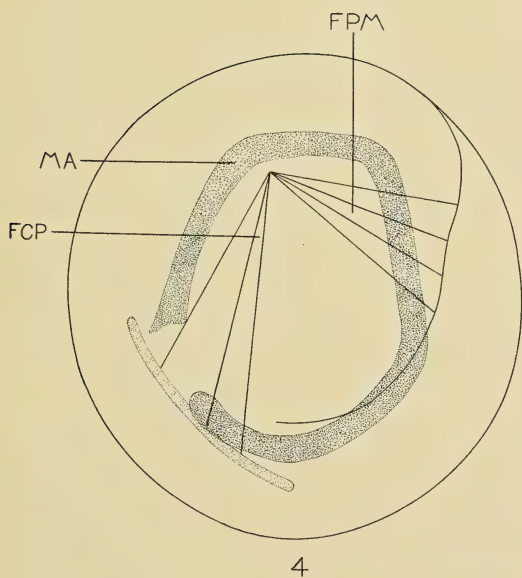
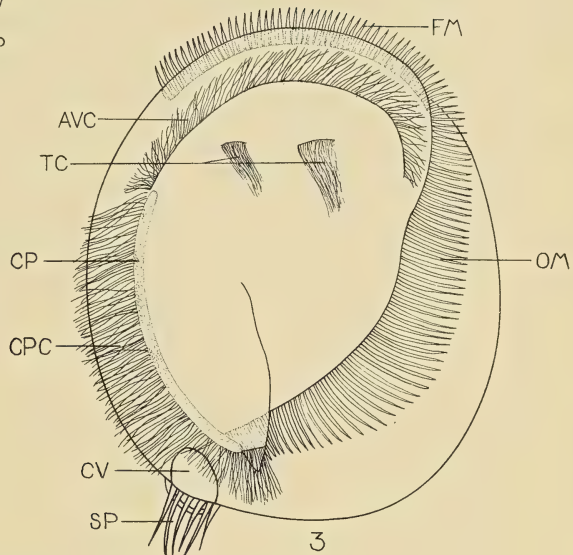
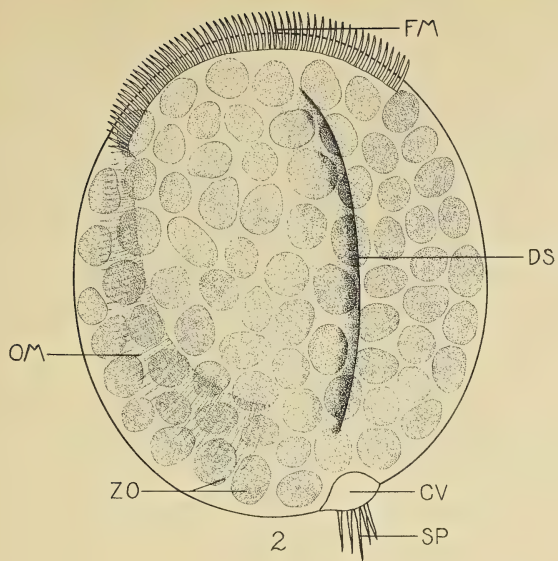
Abbreviations

AVC, anterior ventral cilia	FPM, fibrils of marginal wall of
CP, ciliary plate	peristomial membranelles
CPC, ciliary plate cilia	MA, macronucleus
CV, contractile vacuole	OM, oral membranelles
DS, dorsal swelling	SP, spines
FCP, fibrils of ciliary plate	TC, tufts of cilia
FM, frontal membranelles	ZO, zooxanthellae

Fig. 2. Dorsal view of living organism, showing general shape, structure, and closely packed zooxanthellae.

Fig. 3. Ventral view of living organism, showing ciliation and structures found on that surface. Zooxanthellae not shown.

Fig. 4. Ventral view of ciliate stained with aceto-carmin to show macronucleus and fibrils.



FIGURES 2 TO 4

VI

THE ECOLOGY OF THE VEGETATION AND TOPOGRAPHY
OF THE SAND KEYS OF FLORIDA

By JOHN H. DAVIS, JR.

Southwestern College, Memphis, Tennessee

With seven plates and thirteen text figures

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THE ECOLOGY OF THE VEGETATION AND TOPOGRAPHY OF THE SAND KEYS OF FLORIDA

INTRODUCTION, SCOPE, AND PROCEDURE

This investigation is a study of the vegetation and some of the physiographic features of about thirty of the islands of the Florida Keys, in an area extending west from Key West, Florida, and including the Dry Tortugas Keys. It is part of a series of studies of the plant ecology of southern Florida, the first of which dealt with mangrove vegetation and its significance in land building along the many inundated shores of this region (Davis, 1940). A third study, on the Florida Everglades and adjacent areas, is in preparation. These three together constitute a comprehensive investigation of most of the types of vegetation of this nearly unique subtropical and south-temperate region of the United States.

The islands considered here have been previously studied and described by Millspaugh (1907) and Bowman (1917, 1918). Millspaugh refers to them as the Sand Keys, and since this name is an apt one, it will be used here. Two atolls, namely the Marquesas Keys and the Tortugas Keys, and a group of small islands near Key West compose the Sand Keys. Because of their relative isolation, small size, and subtropical location, these islands are very favorable microcosms for the study of a number of insular problems, particularly vegetational changes. With Millspaugh's, Bowman's, and the present description, a series of observations will be available that will not only show past changes, but furnish a basis for future studies.

Both the mangrove-swamp and the sand-strand vegetation of these islands are also typical of many mainland shores and islands throughout the tropics. The plant communities of which these two types of vegetation are composed are often ecologically equivalent throughout the world, though the floras of different regions may differ. Therefore, this description of the strand and mangrove vegetation here may contribute to other studies of the plant ecology of tropical shores.

Most of the field work in this investigation was done during the summer of 1940, but a number of trips had been made to the region during 1937 and 1938, and a final brief study of winter conditions was made in February 1942. All the islands except six, in the group nearest Key West, were visited, the plant communities of which the vegetation is composed were studied, and some of the environmental factors were analyzed. Familiarity with the flora and the types of vegetation of other islands of the Florida Keys speeded the work. For the purpose of studying physiographic features, particularly topography, a simple method of plane-table surveying was used and maps of the topographic and vegetational features were made. On each

island a fairly accurate survey of the beach part of the coast was made, and where practicable, surveys were run inland from the beach. To these field data were added features obtained from the charts of the U. S. Coast and Geodetic Survey. Unfortunately no good recent charts are available and no aerial photographs could be obtained, so that the drawings given here are not so accurate as might be desired, as regards details. For this reason only major changes in shape, size, and elevation are considered.

The descriptions and drawings given by Millspaugh and Bowman were compared with the observations and surveys of this investigation. Certain definite trends in the development of the vegetation could be noted. Topographic changes were more difficult to estimate because, although Millspaugh's floristic descriptions were fairly complete, the drawings made for him by Lansing seemed to be very inaccurate in a number of instances. Bowman's study (1918) concerned only the vegetation of the Tortugas Keys, but his descriptions and maps were more accurate than Millspaugh's, so that the comparisons between past and present conditions in the Tortugas group are more significant than for the other islands.

Although this was not essentially a floristic study, but rather one of the vegetational units or plant communities, the islands were small enough and the flora of sufficient uniformity for a nearly complete determination of the plant species. To determine the quantitative floristic features of each of the plant communities, the relative frequency, constancy, exclusiveness, and other features of the species were studied. Transects and quadrats were used to obtain quantitative data. In addition, care was taken to find: (1) additions to or deletions from the flora; (2) changes in the major floristic features of each community; (3) some of the probable modes of dispersal of the plants. Dispersion was much emphasized by Millspaugh, but not enough data were obtained in this study to make possible more than a few observations in this connection.

Time and equipment were not sufficient to make very comprehensive studies of the environmental factors, but enough was learned of the most important ones to permit some significant analyses of environmental relations. Many persons have studied maritime conditions in this region, and some of their observations and conclusions were helpful in explaining the principal factors in the formation and development of these islands.

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PART I. GENERAL DESCRIPTION

LOCATION, TOPOGRAPHY, AND GEOLOGY

The thirty-odd islands of the Sand Keys lie between $81^{\circ} 48'$ and $82^{\circ} 56'$ west longitude, and between $24^{\circ} 30'$ and $24^{\circ} 40'$ north latitude. They are scattered over an area west of Key West, about 70 miles from east to west and 9 miles from north to south. As is shown in figure 1, the islands are in three fairly distinct groups: (1) a group of fourteen islands extending 11 miles west of Key West; (2) a group forming the Marquesas Keys, an elliptic atoll 17 to 20 miles west of Key West; and (3) the most distant group, the Dry Tortugas Keys, 65 to 70 miles west of Key West.

The group nearest Key West bears no special name, but most of the islands of which it is composed are named on the charts or by natives of the region. These islands are slight elevations above a broad bank of oölitic limestone that extends westward from Key West harbor to the Boca Grande Channel. The southernmost islands of the group are arranged in a slightly curving chain from east to west, along the southern rim of the limestone bank. The other islands are scattered over a wide area to the north.

The Marquesas Keys are based on the same bank of oölitic limestone, which is called by some the Key West limestone and by others the Miami limestone. This great bank is an extension of the formation that underlies Florida Bay and forms the westernmost of the Florida Keys from East Bahía Honda Key to Key West. The limestone extends as a tongue-like plateau beyond the Marquesas Keys and possibly dips down and underlies the banks and reefs on which the Tortugas Keys are built. A distinct channel, the northwest channel out of Key West harbor, cuts across the bank and separates the islands near Key West from the main chain of the Florida Keys. A broader and deeper channel cuts northward across the bank between Boca Grande Key and the Marquesas Keys. Between Rebecca Shoal, west of the Marquesas Keys, and the Tortugas Keys there are many miles of deep water, the bank if present dipping sharply. Over much of its area this submerged plateau of limestone is so near the surface that parts of it are exposed at the lowest neap tides, and it is possible to wade between some of the islands. This shallow-water bank stands only a few feet higher than the surrounding deeper-water areas and, as Cooke (1939) points out, "appears to have formed as a shoal in the sea during Pamlico [late Pleistocene] time because of the locally more rapid accumulation of limy oölite ooze." Vaughan (1914) interprets the age of this rock differently, and considers it to have formed during the Pliocene. With reference to changes in sea level along this coast, he says: "The evidence is clear that the keys participated in the uplift and subsequent depression that affected the mainland and that at one time they stood more than thirty feet higher with reference to sea-level than they now do. This



Fig. 1. Map of the Sand Keys, with islands drawn to scale except the smaller ones, which are slightly enlarged. Limestone bank near Key West shown by broken line. Islands of group near Key West that were studied: A, Boca Grande Key; B, Man Key; C, Ballast Key; D, Woman Key; E, Barracuda Key. Islands of the Dry Tortugas Keys: F, Loggerhead Key; G, Garden Key; H, Bush Key; I, Long Key; J, Hospital Key; K, Middle Key, now submerged; L, East Key; M, Bird Key, now submerged.

uplift and subsequent depression, according to all available evidence, extended to the Tortugas." Cooke (1935, 1937) and the author are inclined to consider the present level as due to a rise in sea level during Recent time. Whatever may be the best interpretation of the geologic history of this region, the present islands are, with the possible exception of the Tortugas Keys, mainly formed by accumulations of detrital materials washed into certain localities by the currents and resting on this oölite limestone bank. On only one island, Boca Grande Key, is much of the limestone exposed at the surface, most of the other parts of the bank west of Key West being now submerged.

The two atolls of the Sand Keys are most interesting. The ten main islands of the Marquesas group form an ellipse which extends along a north-east-southwest axis and encircles shallows and interior lagoons. The Tortugas Keys are 45 miles west of the Marquesas group and are completely surrounded by deep water. The islands themselves do not form a distinct atoll, but when the banks on which they rest and the banks near them are taken into consideration, the whole formation is seen to be an elliptic atoll similar in shape to the Marquesas atoll, but larger. The main ellipse of the Tortugas atoll is formed by large banks around the rim of deep-water lagoons. The largest of these banks is in the northeast quadrant of the atoll, forming a wide crescent, with one small island, East Key, resting on its southern horn. Another large bank is in the southwest quadrant, and on it rests the largest island of the group, Loggerhead Key.

At both the Marquesas and Tortugas atolls there are three distinct channels which enter the interior basins from the same directions, southeast, southwest, and northwest. At the Marquesas there are no coral reefs, but at the Tortugas living coral reefs abound. Ten distinct and some incipient islands lie around the rim of the Marquesas atoll, but at present there are only six islands in the Tortugas group, two others having recently disappeared. These two atolls were built up by similar currents and constructional processes, which should be considered in some detail in order that their shape and the nature of the islands may be understood.

The marine currents which most influenced the formation of these two atolls, and in a slightly different fashion that of the islands near Key West, are of three kinds: (1) wind-formed currents accompanied by waves; (2) the Florida countercurrent; (3) the tidal currents. The wind currents are prevailing from the east, particularly during the summer months, when these islands are in the latitude of the trade winds. The Florida countercurrent between the Gulf Stream and the Florida Keys flows westward along the southern margin of these islands. The tidal currents are north and south, the strongest being the ebb-tide thrust from north to south. The strongest combined action of these currents forms a northeast current that accounts for the elliptic shape of the two atolls.

This northeast current produces the largest island of the Marquesas group, the long, crescentic Long Beach Key. This current also accounts for the development of the northeast bank of the Tortugas atoll. Both these crescent-shaped formations lie between the northwest channels and the southeast channels that enter their respective atolls. In both cases the bow of the crescent island or bank faces the current, and the horns of the crescent curve before the current. The specific location and shape of the other islands and banks of each atoll may be due to local differences in the currents. Thus in the southwest quadrant of both atolls islands are formed. At the Marquesas Keys the island is Southwest Key, and it bows toward the southwest with its horns extending north and east; at the Tortugas Keys the southwestern island is Loggerhead Key, and it bows toward the southeast with its two horns projecting toward the west. Southwest Key at the Marquesas seems to be due to a countercurrent against the direction of the prevailing northeast current.

The accumulation of the sediments and detrital materials which form the banks and islands of these atolls is the result of constructive processes mainly influenced by the direction and force of the currents, some of which are general and some very local. In general the outer faces of the islands around the Marquesas atoll receive the strongest currents and wave action, which cause the coarsest materials to pile up on these outer faces. Finer materials are deposited on the lee or inner sides of the islands, in the quieter waters inside the atoll. Consequently the inner faces of the islands are mud flats covered by mangrove swamps, and the outer faces are beaches and dune plateaus covered by strand vegetation. This condition does not, however, prevail at the Tortugas atoll, where nearly all the materials are coarse and few fine sediments accumulate to form mud flats. All the Tortugas islands are formed of coarse detrital material carried by currents so strong that shifts in them have caused the destruction of some of the islands and rapid growth of others.

It is more difficult to explain the location, shape, and other topographic features of the islands that form the group near Key West. All the southernmost islands except Crawfish Key have beaches and dune plateaus along all or part of their southern shores. Woman and Man keys are distinctly elongated in an east-west direction. The other islands of the group are scattered north of this southern row over the very shallow waters of the limestone bank. None of these latter islands have any distinct beaches or dune plateaus. At most they have low sand and marl ridges and interrupted narrow beaches. Most of them are completely or almost completely covered by the tide and support a mangrove vegetation.

Irregularities in the surface of the limestone bank and differential erosion by the north-south thrust of the tidal currents seem to account for the development of these islands. The largest island, Boca Grande Key,

developed around a raised limestone shelf which forms a central plain (pl. 2, fig. 2). Sands have accumulated around the western and southern parts of this rock plain, and muds around most of its northern and eastern shore. Woman Key is likewise based on exposed rock. In general the southern rim of the bank on which these islands are based is dissected by north-south channels, with segments of the bank between them. Erosion by tidal scour probably caused the channels, and the elevated segments between them were appropriate places for the accumulation of detrital materials. Thus the highest parts of the limestone bank, left in the segments, form the bases for the islands and the many areas of shoal water along this southern rim. The islands resulted from or were enlarged by deposition of coarse material borne from the south and east, forming sand beaches and dune plateaus along their southern shores. Finer materials, mostly marl muds, accumulated on their northern or lee sides, forming mud flats. The currents from the east aided in forming the two elongated islands, Man and Woman keys. At Boca Grande Key the southern and the western shore are both sandy, the latter probably because of currents sweeping toward the island from the Boca Grande Channel to the west.

Over the middle and northern parts of the limestone bank near Key West the low, mangrove-covered islands probably developed where there were local retardations in the currents, or slight elevations of the bank, or both. The shoal areas of this region are very shallow, and mangrove colonies once fixed in the mud could easily start a mangrove island. Since most of the islands are partly or completely flooded by normal high tide, they are not islands in the true sense of the word, but merely mangrove swamps.

The coarse calcareous sands of parts or all of the islands composing the three groups are the result of accumulation of unconsolidated detrital material. At the Tortugas Keys some of this material is from coral reefs, but coral fragments contribute little or nothing to the formation of the other islands. Fragments of calcareous algae, particularly species of *Halimeda*, contribute a great deal to these sands, especially at the Tortugas; and a great variety of other organisms that secrete calcium carbonate, such as mollusks, foraminifera, echinoids, and nullipores, also furnish detrital material.

Sorting by the currents results in the different types of accumulation on the bottom, on the sand strand, and on the mud flats. From a study of many bottom samples in this region, Thorp (1935) showed how currents sort out and carry along these materials, depositing those of different sizes and weights at different places. The distribution of particle sizes in the various regions of the Florida Keys conforms to the general current conditions. Thus, strong wave and current action brings about removal of most of the silt and clay particles from the sediments, with good sorting of the sand grades. The strength of wave and current action in general increases

westward, and consequently the sands become coarser and more abundant than silts or clays westward, until at the Tortugas Keys there are only a few fine sediments in the troughs of the lagoons. The protected flats on the lee sides of other islands are in general covered by fine-grained sediments, and the sands are deposited on the sides where the currents and waves are strongest. Lagoon and channel deposits have coarser-grained material on the slopes and tops of the ridges. The topography of each island, as well as the nature of the sands and finer materials that make them or are adjacent to them, depends on this sorting action of the currents.

Thus we see that marine currents are the main agents in island formation and vegetation plays a secondary role. Vegetation, however, alters or maintains the topography of each island; the currents account only for the initial stages and the shore-line features. Waves and tides cast up the sands that form the beaches and dunes, but strand plants quickly aid in the stabilization of these sands so that against them other sands can be deposited. Fine-grained materials settle out in slack water to form mud flats, and mangroves growing on these flats hasten the process of deposition, adding some of their own organic materials to the accumulating swamp soils and often forming deep layers of peat and marl (Davis, 1940). Thus both the strand and mangrove plants materially aid in the holding of these unconsolidated materials. They may not cause major constructional changes in either shape or elevation, but without them there certainly would be greater destructional changes, especially those due to excessive erosion during storms. Both these types of vegetation and their influence on the topography of the islands will be considered in detail.

THE PLANT COMMUNITIES

Introduction

The two distinctly different types of vegetation are (1) the mangrove swamps and (2) the sand-strand vegetation. As was pointed out above, both these types of vegetation are not found on every island, but whether on the same island or on separate islands, they occur on soils that are distinctly different in elevation and texture. The soils most favorable for the development of the strand vegetation are coarse sands at elevations above the usual high tide, whereas the most favorable soils for mangroves and associated salt-marsh plants are fine-particled sediments, mostly marl, that are usually or constantly flooded by the tide. The plant communities of which the two types of vegetation are composed are distinct as regards nearly all their species and the growth form of most of these species. (See "Plant populations," under "Flora," below.) Their one main point of similarity is that each type of vegetation is composed of a series of communities forming a fairly definite succession which is in many places con-

tributing to topographic changes. The communities of each of these successions, or seres, are often arranged in fairly definite zones from the open water inland. The final development of each sere is toward a similar mesic, non-flooded, non-saline-soil type of vegetation, as is shown diagrammatically in figure 2. Each of these seres begins with a halophytic

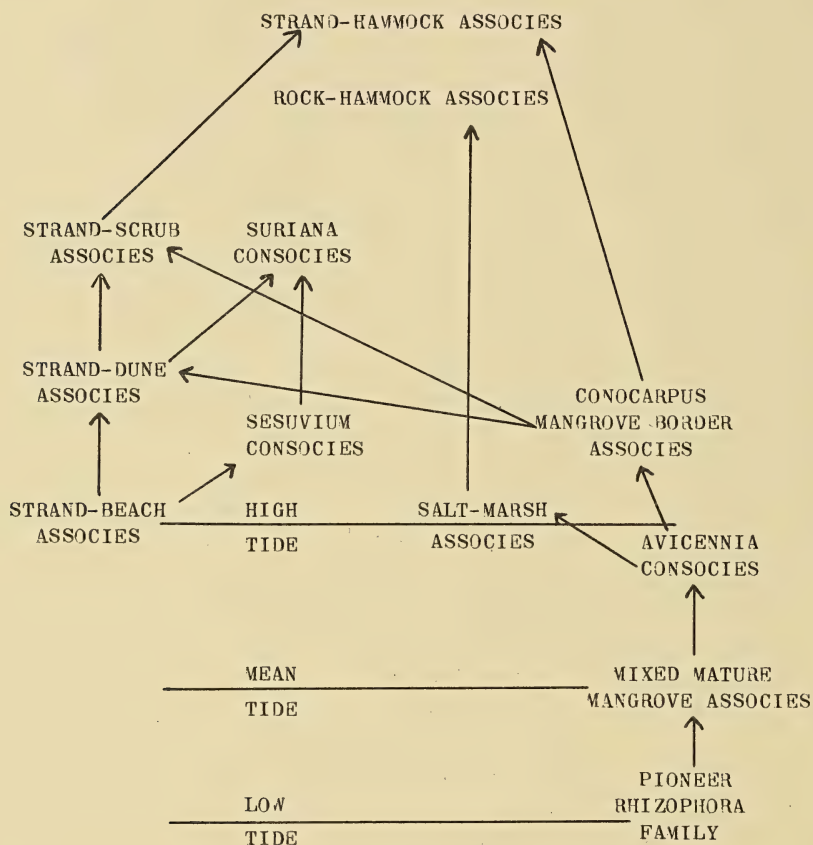


Fig. 2. Successional relations of the strand and mangrove communities. Approximate tide levels are indicated.

pioneer community, but there their similarity ends. The mangrove succession is a halic hydrosere from constantly flooded soils inland to levels only slightly above the usual high tide, whereas the strand succession begins on the upper beach, which is only occasionally flooded, and is a partly halic, partly xeric psammose, the zones of plant communities occurring in successively less saline, usually more mesic, and more elevated situations.

As described in the discussion of mangroves (Davis, 1940), the mangrove

succession may develop into an upland, non-halophytic forest known locally as a hammock. The strand sere even more often develops toward such a hammock forest. Both may develop toward and contribute soils for the near-shore hammock forests. Although the two successions proceed much as shown in figure 2, in many parts of the whole chain of the Florida Keys they do not always develop fully on each island. In only one instance, Long Beach Key, does the strand succession attain a well developed hammock stage, and in only a few instances is there a well developed transition from mangrove swamp to hammock forest that may be the direct result of soils accumulated in the mangrove swamps.

This study was undertaken partly to determine the essential features of the strand communities, since the mangrove communities had been previously studied. For this reason the ecology of the strand communities is stressed. A general description of the ecology of both types of vegetation and some of the most important factors of the habitat precedes the descriptions of the communities of each island.

The Strand Communities

The strand vegetation and strand flora of the Sand Keys are similar in many respects to those of the sandy shores of the mainland coasts and of the many islands of southern Florida, except that the flora includes more tropical species. These islands are comparatively small, and the communities are often confined to distinct areas which form definite zones along the shore. There is usually a very definite line of demarcation between the sand areas and the mud flats, so that there is an abrupt transition from the strand communities to the mangrove communities. Some of the islands of the group nearest Key West have no strand vegetation, and all the islands of the Tortugas Keys are covered by strand communities with only a few small colonies of mangroves.

The four main communities recognized as composing the strand succession are: (1) the pioneer strand-beach associates, from the wave line on the beaches to the higher parts of the fore dunes, definitely above the usual effects of the tide and waves; (2) the strand-dune associates, occupying the fore part of nearly all the dune plateaus, composed of grasses, low shrubs, and herbs; in this region this plateau is usually dominated by the tall sea oats, *Uniola paniculata*; (3) a transition community, the strand-scrub associates, of low shrubs and small trees scattered over the inner parts of the strand-dune areas, and typically including some species of distinctly xeromorphic adaptations, indicating the xeric conditions of the habitat; (4) the strand-hammock associates, which is a strand forest of low trees and shrubs growing in a close stand and composed of many species of tropical hardwoods and palms. These latter communities are the shore hammocks or

sand hammocks. They are not so well developed on these small islands as on the larger islands or the mainland. On only a few of the islands studied are all four communities found well developed and distinctly arranged in zones. On many of the islands, particularly of the Tortugas Keys, there are variations in the plant populations of these communities, and local aggregations of certain species to form associates, colonies, and families. In some instances the individual plants are so scattered over the strand sands that no definite community can be recognized. The most constant and frequent species of each community are summarized in tables 1, 2, and 3.

A number of similar strand communities have been recognized in other studies of strand vegetation in this and other parts of the world. Raunkiaer (1934) in his description of some of the Danish islands of the West Indies recognizes even more zones, facies as he calls some of them, of both the sand-shore and the mangrove-swamp vegetation. For the Malay region, Schimper in his classic work *Die indo-malayische Strandflora* (1891) gives good accounts of the beach and dune vegetation. In these and many other instances there has been a tendency to divide the strand vegetation into components based too specifically on the plant populations. Here that tendency has been avoided so far as possible, but could not be entirely avoided because of the necessity of specifying the dominants of a community. In general, the terms strand beach, strand dune, strand scrub, and strand forest (here hammock) might be more or less universally applied to the vegetation of sand shores.

The strand-beach associates is composed of a number of pioneer halophytic species that can spread out over the upper beach, take root quickly, germinate from seeds rapidly, and withstand some wave wash and sand shifting. The commonest species are *Sesuvium portulacastrum*, *Cakile lanceolata*, *Ipomoea pes-caprae*, *Panicum amarulum*, *Sporobolus virginicus*, *Uniola paniculata*, *Chamaesyce buxifolia*, and the shrub *Tournefortia gnaphalodes*. Other species are named in the descriptions of the islands and in the summary of species given in table 1. It is necessary for these upper-beach plants to withstand occasional submergence, and therefore they are the most halophytic species of the strand. The typical species are not confined to the upper-beach and dune areas, but may occur within the strand-dune associates. In fact two of them, *Uniola* and *Chamaesyce*, are the main dominants of many strand-dune areas. Most of the beaches on these islands are so narrow and the dune terraces so close to the upper reaches of the tide that the pioneer strand-beach plants fail to develop. Where developed, this associate indicates aggradation of the beach, as the plants are the first to grow on newly built-up sand areas.

The strand-dune associates is the commonest and most distinctly zoned of the strand communities. It covers the fore part of the low dune areas, from 1 to 9 feet above the high-tide level. Generally there is a steep

wave-cut terrace and the dunes are low, almost flat areas, forming a plateau. If these low dunes are wide, three stages in the strand succession may be developed. The strand-dune associates is the outermost or first in the succession, and is the most prevalent of these communities. It is usually a narrow zone 25 to 150 yards wide. Unless the plateau is more than 75 yards wide, it is nearly always entirely covered by this associates, the strand-scrub and strand-hammock communities failing to develop.

The strand-dune associates is dominantly herbaceous (pl. 1, fig. 2), with *Uniola paniculata*, other grasses, *Waltheria*, *Chamaesyce*, a number of leguminous plants, and the spider lily, *Hymenocallis*, as frequent associates (table 1). The two commonest shrubs, *Tournefortia* (pl. 2, fig. 1) and *Suriana*, are not constant, some islands having few of them and others many. In fact, *Uniola*, although the most frequent plant in most of these strand communities, is almost absent from one part of the Woman Keys. Millspaugh (1907) noted this variability in the floral composition of the strand. The difference in local abundance of the species has no general effect on the character of the community, unless there is a definite increase in the number of shrubs. The community is considered unaltered where shrubs are scattered over the strand-dune area, but where they become abundant and cover more of the area than the herbs, a strand-scrub associates is recognized.

The strand-scrub associates is typically a transition zone between the strand-dune associates and the hammock forest, if a hammock forest is developed. On most islands, however, there is no well developed strand-hammock associates, so that the scrub associates occupies the inner zone of many dune plateaus. *Suriana maritima* is the most frequent species. At the Tortugas Keys *Suriana* is the dominant vegetation of the larger islands, forming a distinct consociates, which is one form of the strand-scrub community. On most of the Marquesas Keys, Barracuda Key, and the western half of the Woman Keys, on the sand ridge back of the mangrove border or on the inner part of the strand plateau there are thickets of a number of species of strand-scrub plants. *Suriana*, *Lantana*, *Guilandina*, *Solanum*, *Borrchia*, and *Opuntia* are frequent and typical. The open areas between the colonies of scrub plants have a number of plants that are common in the strand-dune associates. A few hammock plants such as *Jacquinia*, *Coccothrinax*, and *Pithecolobium* are often present. Not a few of the scrub areas are probably slowly changing to hammock areas.

The prevalence of this xeric scrub community on the strand between the more halic strand-dune associates and the more mesic strand-hammock associates is probably due to the extreme porosity of the coarse sand soils and to the small, seasonal rainfall. The gradual change of the soil solution from distinct salinity near the beach to only a trace of salinity farther inland is accompanied by a gradual reduction in soil moisture; then as humus accu-

mulates, the soil moisture, at least near the surface, increases, with a consequent development of more mesic conditions in some places, promoting hammocks. The strand scrub develops on the soil areas with least water content between the shore and the hammock forest or mangroves. The drier condition of the Tortugas islands, due both to the small rainfall and to the coarse soils, probably explains the failure of hammocks to develop there. In other localities also, mesic conditions for hammock growth have failed to develop.

The climax development of the strand succession is the strand-hammock forest. On these small islands no real climax hammock association has developed, as has occurred on some of the other Florida Keys. The nearest approach to this condition is on Long Beach Key; there are less well developed hammocks on Boca Grande and Southwest keys. These communities are thicket forests, composed for the most part of small trees, but with some larger ones, over 30 feet tall. A few of the species here are also typical of the tall tree hammocks of the shores of larger islands. Some of the significant genera of this climax strand associates are *Pithecolobium*, *Jacquinia*, *Coccothrinax*, *Thrinax*, *Metopium*, *Reynosa*, *Capparis*, *Eugenia*, *Torrubia*, and *Epidendrum*. Whether or not this associates will finally develop into a larger forest of more species and more definitely climax characteristics will probably depend on the continued enlargement and stabilization of the islands.

All the hammock plants are not on sand; a hammock community has developed on rocky soils on one island, Boca Grande Key (pl. 2, fig. 2). The plants are dwarfed, scrubby, and widely spaced like those of the strand-scrub associates, but the species are the same as or similar to those of many of the sand-strand hammocks. Some plants, for example *Opuntia*, *Gossypium*, *Bumelia*, *Maytenus*, *Pithecolobium unguis-cati*, and *Cordia* (table 3), are more typical of rock hammocks and marl soils than of sand hammocks. On the larger Florida Keys these rock and marl hammocks are common. This one community is only a small, poorly developed example.

The distinction between rock hammock and sand hammock is made here largely for convenience. The two are very similar, in fact both are shore or key communities common to most of the western Florida Keys, where oölite limestone rock, marl, and sand soils are all so general and so contiguous that the same plants grow on all to form essentially the same ecological unit.

To aid in a better understanding of the development of a key hammock association, the most frequent species of some hammocks on the islands near Key West are listed in table 3. Tropical hammocks are so variable in plant composition that no general statement can be made. The table gives only a few of the many tree and shrub species to be found on the Florida Keys. Small (1913) and many others have stressed this diversity of the flora of

this region. Such diversity is in part due to great differences in ecological conditions. The poorest tree flora of the region is on these Sand Keys, no doubt because of the small size of the islands, low rainfall, and dominantly coarse sandy soils.

The Mangrove Communities

The mangrove succession, the typical communities of which it is composed, the environmental factors, and something of the manner in which soils are built up in the swamps have been described by the present writer (1940) and need not be treated in detail here. There are, however, a few distinctive features of the mangrove swamps of the Sand Keys which should be especially noted.

In general the mangroves occur on the shoals near the islands and on the inundated parts of the islands away from the direction of the prevailing currents (pl. 1, fig. 1). In such locations the finer sediments accumulate over the rocks and in the swamps, forming the best habitat for mangrove growth. Only occasionally do mangroves grow on parts of the sand beaches, and then only where there is little wave action. The low brackish-water flats in the interior of some islands are usually covered by mangroves and by an associated salt-marsh vegetation. Those islands that have failed to develop beach and dune areas are usually completely covered by mangroves. Other islands, especially the Tortugas Keys, have few or no fine sediments or flooded parts, and on them few or no mangroves occur. The most prevalent condition is a combination of mangrove swamps and strand vegetation on the same island. There is usually a sharp demarcation between the two. As the sand soils slowly migrate inland they often form a steep bank or terrace at the edge of the depressions filled with mangroves. This terrace may encroach on the mangroves and cover some of their roots. Along this border zone there may be developed a narrow border associates of plants, with some species from each of the two types of vegetation. On the higher soils the buttonwood, *Conocarpus erecta*, sometimes grows and becomes an important element of the strand flora. Some of the strand plants occasionally invade the mangrove swamps.

The total areas covered by mangrove communities are much greater than those covered by strand communities, but since most of the mangrove areas are submerged soils, it is not possible to describe all of them as land. Some of the smaller mangrove colonies on the shoals are not islands, for they have no areas above even the low tide. It is impossible to distinguish rigidly between sea and land areas. The outlines shown on the maps of the mangrove parts of the islands, and of the completely mangrove-covered islands, are at best approximations of the border of the mangrove growth and in most cases include flooded areas. For this reason it is impossible to give the exact number of the islands or the area of many of

them. If only the sand-strand areas were considered as islands, many of the islands would appear much smaller in the figures, and some of them would not be shown at all.

The mangrove swamps of the inundated shores and the mud flats are composed of three species: *Rhizophora mangle*, the red mangrove, *Avicennia nitida*, the black or honey mangrove, and *Laguncularia racemosa*, the white mangrove, sometimes called the white buttonwood. *Conocarpus erecta*, the buttonwood, is associated with both the strand and the mangrove communities, being frequent along the border between the two. The communities, their species, and the associated plants form less clearly defined zones than those described for the southern Florida region in general (Davis, 1940). On these islands there is less variety of conditions of water and soil than is found on larger islands and the mainland, where a complete development of the mangrove succession from a pioneer *Rhizophora* family through the stages of a mature *Rhizophora* consocieties, *Avicennia* salt-marsh associates, and *Conocarpus* transition associates to an upland inland hammock forest or to a fresh-water swamp community may occur.

The mangroves in the deepest-water parts of the swamps are mostly *Rhizophora*. On many shoals there are distinct pioneer *Rhizophora* family communities of young red mangroves. A number of the larger swamps are mature *Rhizophora* consocieties of medium-sized trees forming a very thick stand. With *Rhizophora* there are often many *Laguncularia* and *Avicennia* trees, forming a mixed growth that might best be described as a mature mangrove associates, or in young stages a mixed mangrove colony. In general, *Avicennia* forms a distinct community in the shallow-water parts of the swamp, and *Laguncularia* grows along the outer fringe of the swamp.

The largest *Avicennia* communities cover stagnant-water flats in the interior of the islands, particularly around ponds, as on Barracuda and Boca Grande keys. These swamps are thicket growths of small and medium-sized trees with little or no salt-marsh herbage beneath them. The few salt-marsh species do not form as definite a salt-marsh flora as is usually the case in southern Florida; *Batis* is the only plant commonly associated with *Avicennia* here. For this reason most of these communities are an *Avicennia* consocieties. The water in this zone of the swamp averages about 6 inches deep, is not normally affected by the tide, and becomes alternately very salty and diluted with rain. On thin soils over rock substrata the trees are scrubby and widely spaced, forming a scrub *Avicennia* community.

Similar mangrove flats of a scrubby growth of *Rhizophora* occur over the interior flats of some islands, so that a scrub *Rhizophora* facies is recognized. This is a scrub *Rhizophora* consocieties.

There is no distinct *Conocarpus* transition zone, and there are not many evidences of a complete series of the mangrove communities, forming distinct zones. Not many of the swamps have deep organic soils. There is

some peat development, but most of the swamp soils are marl muds with some calcareous sands, and the rock substratum is usually near the surface. No doubt this sedimentary and partly cumulose soil is developing a halotropic series, but there has not been sufficient time for the development of deep soils with distinct profiles such as are found in some of the large swamps of the mainland and some of the larger Florida Keys (Davis, 1940, p. 387). Mangroves are contributing mainly to increasing sedimentation of muds on the lee sides of the islands, and somewhat to the building up of the soil levels high enough for the coarser sands to collect over the marl muds. In this way they contribute to the gradual extension and elevation of the islands.

In the Marquesas Keys, the inner faces of all the islands, toward the lagoons, are covered by mangroves. Most of the outer faces of the elevated parts of the islands have narrow beaches and a plateau dune area covered with strand vegetation, but many of the lower islands, and low parts of others, are entirely covered by mangroves. Similarly there is usually a mangrove side and a strand side on the islands near Key West, but many of them are completely covered by mangroves. Consequently each island has its own distinct areas of mangrove vegetation and must be considered individually.

Some of the shores of coarse sand soils with some marl, but of low relief, have fringing mangroves in the shallow tidewater offshore from the bare sand beaches. In a number of places these mangroves have grown inland, covering the beaches and invading the strand vegetation. Such pioneer mangrove growth is common around the southern and eastern shores of the Marquesas Keys. Extension of mangroves along the beaches seems to be increasing because of the accumulation of finer soil materials offshore or on the beaches; and their growth is causing a decrease in the intensity of wave action on the beaches or shoals near them. Along many shores of these islands there are long areas of sand beaches not interrupted by mangrove growth, but on some, shores facing in the same general direction as those with beaches are dominated by mangroves. Where mangroves predominate along a shore, but there are also a few short areas of sand beach and pioneer strand plants, the shore is known as one of broken beaches. This is the case around much of Barracuda Key and the eastern shore of Long Beach Key.

Back of an outer shore fringe of mature mangroves of all three species there is frequently a low ridge of mixed marl, shell, and sand soil between the open water and the shallow, flooded interior swamps. This ridge is above the tide level and on it grows a mixture of mangroves and salt-marsh and strand plants. As the larger mangroves shade the ridge, the plants grow under fairly mesic but also halic conditions. This mixed community contains large *Conocarpus* trees, *Borrchia*, *Sesuvium*, *Hymenocallis*, *Iva*,

Dondia, and some of the strand-scrub plants such as *Lantana* and *Solanum*.

Most significant is the lack of mangrove swamps at the Tortugas. Seeds and seedlings of all three species float there by the thousand, and some of them become rooted on the beach, only to die from excessive exposure. A few grow on the coral ballast of Long Key. Only around one pond on Bush Key is there a mangrove swamp, an almost pure consociation of *Laguncularia* with a few *Rhizophora*.

The relations of the mangrove communities are shown in figure 2. In general, the few differences between the communities and successional relations of mangroves on these islands and those along the south Florida coast are not significant. Here the mangrove swamps are less distinctly zoned, soil development is less advanced, and the final stages of the succession are not apparent. The mangroves of the Sand Keys contribute something to the acceleration of sedimentation, and enable sands to accumulate more rapidly by damming up water currents. There is a gradual change from mangrove-swamp areas to sand-strand areas with the filling in of some of the swamp areas by sands blown in over them.

FLORA

Plant Populations

About 110 species of plants are commonly found in the strand vegetation communities, but less than 15 species are frequent in the mangrove swamps and salt marshes. The total is a relatively small number of species for so large an area, and the number is even smaller, probably not over 80, if only the definitely native plants are considered. This relative paucity of the flora is typical of isolated small islands. The environmental conditions are such that few plants can become established, and the isolated position makes it necessary for the plants to migrate some distance. The ability of the plants to migrate is of particular importance in determining the composition of the flora. Millspaugh (1907) gave a number of "Distributional notes" concerning the mode of dispersal of the plants, but in the present investigation only a few such observations were made. Some of these will be considered later.

The plant population of each community was determined by the use of many sample plots, both quadrats and transects, which in each instance were located where that particular community seemed best developed. Besides these detailed studies on some of the islands, notations on the species and their relative abundance were made for all situations on each island visited. The main object was to obtain the relative frequency or abundance of the species, the constancy of the most frequent and dominant, and the exclusiveness of some of them. From these data the tables of the flora of each

community were made (tables 1, 2, 3). In most instances the ten or fifteen most frequent and constant species are listed in order of their relative frequency and constancy, then an alphabetical list is given of additional plants. Each list does not include all the species found, and a very few that were present, particularly grasses without flowers or fruits, have not yet been adequately identified.

The ten most frequent species of one sample plot of a particular community are often not present in the same abundance in other sample plots on the same island, or different islands. A few species are confined to a definite location owing to chance distribution. This exclusiveness, in some cases endemism, is typical of the south Florida region, particularly of the islands. Species of palms, for example *Coccothrinax argentea* (Lodd.) Sarg. and *Thrinax microcarpa* Sarg., are very local in their distribution. Almost every island with a strand flora has some species not present, or very rare, on other islands. This lack of constancy makes it difficult to give a description of the plant population of any one associates that will hold for all the islands. For this and other reasons, only the most general descriptions of the associates have been given above, and the details of plant populations are given later with the description of each island.

The plant names employed by Bowman and Millspaugh in their lists of the flora, and the names used in the best available manual for this region (Small, 1933), are not always the same. This synonymy of names makes it difficult to list properly all the species found. In general the names given here conform with Small, except in certain cases where his names are used little or not at all by students of this region.

One of the interesting features of the flora is the much greater diversity of the flora of the strand than that of the mangrove swamps and salt marshes. The strand flora is of many families of herbs and low shrubs, mainly grasses, legumes, spurges, purslanes and their kin, amaranths, and Compositae. The shrubs and trees of the strand scrub and strand hammock belong to many different families familiar in the tropics. In contrast with this variety, the commonest mangrove and salt-marsh plants belong to only six families. This condition seems due mainly to the fact that the mangrove swamps and salt marshes, being partly or completely inundated and distinctly saline, are not so favorable for the temporary establishment of plants as are the sand areas. Many ruderals, ballast plants, and other weeds become established on the strand (table 7, p. 182). In a number of instances these are abundant locally but completely absent elsewhere, indicating chance distribution. Additions to the strand flora occur from time to time, and certain species seem to have been lost from the flora since Millspaugh's account.

Table 1. *Plant populations of the grass and herb communities of the strand*

<i>Strand-beach associates</i>	<i>Strand-dune associates</i>
In order of frequency and constancy	In order of frequency and constancy
<i>Sesuvium portulacastrum</i> L. <i>Cakile lanceolata</i> (Willd.) Schulz. <i>Cenchrus pauciflorus</i> Benth. <i>Chamaesyce buxifolia</i> (Lam.) Small <i>Uniola paniculata</i> L. <i>Iva imbricata</i> Walt. <i>Panicum amarulum</i> H. & C. <i>Sporobolus virginicus</i> (L.) Kunth <i>Tournefortia gnaphalodes</i> R. Br. <i>Ipomoea pes-caprae</i> (L.) Sweet <i>Scaevola plumeri</i> Vahl <i>Andropogon glomeratus</i> (Walt.) B. S. P. <i>Cyperus brunneus</i> Sw. <i>Portulaca oleracea</i> L. <i>Suriana maritima</i> L. <i>Dondia linearis</i> (Ell.) Millsp. <i>Borrichia arborescens</i> (L.) DC. <i>Ambrosia hispida</i> Pursh <i>Atriplex arenaria</i> Nutt. <i>Batis maritima</i> L. <i>Chloris petraea</i> Swartz. <i>Melanthera hastata</i> Michx. <i>Paspalum caespitosum</i> Flugge <i>Flavaria linearis</i> Lag. <i>Poinsettia pinetorum</i> Small <i>Tithymalus Smallii</i> (Millsp.) Small	<i>Uniola paniculata</i> L. <i>Chamaesyce buxifolia</i> (Lam.) Small <i>Andropogon heteroflorus</i> (Nees) Kunth <i>Waltheria americana</i> L. <i>Cyperus brunneus</i> Sw. <i>Hymenocallis keyensis</i> Small <i>Canavali lineata</i> (Thunb.) DC. <i>Iva imbricata</i> Walt. <i>Flavaria linearis</i> Lag. <i>Spartina patens</i> var. <i>junceae</i> H. Hitchc. <i>Ambrosia hispida</i> Pursh <i>Melanthera hastata</i> Michx. <i>Suriana maritima</i> L. <i>Tournefortia gnaphalodes</i> R. Br. <i>Bradburya arenicola</i> Small <i>Galactia spiciformis</i> T. & G. <i>Poinsettia pinetorum</i> Small <i>Scaevola plumeri</i> Vahl <i>Sesuvium portulacastrum</i> L. <i>Sporobolus virginicus</i> (L.) Kunth <i>Chloris petraea</i> Swartz. <i>Chamaecrista aspera</i> (Muhl.) Greene <i>Achyranthes maritima</i> (Mart.) Standl. <i>Sporobolus domingensis</i> (Trin.) Kunth <i>Caesalpinia pauciflora</i> (Gris.) Wright
	Additional species in alphabetical order
	<i>Atriplex arenaria</i> Nutt. <i>Batis maritima</i> L. <i>Bidens leucantha</i> L. <i>Borrichia arborescens</i> (L.) DC. <i>Calonyction tuba</i> (Schlecht.) Colla <i>Capriola Dactylon</i> (L.) Kuntze <i>Cenchrus pauciflorus</i> Benth. <i>Cenchrus tribuloides</i> L. <i>Chamaesyce hypericifolia</i> (L.) Small <i>Chloris glauca</i> (Chapm.) Vasey <i>Dondia linearis</i> (Ell.) Millsp. <i>Eragrostis ciliaris</i> (L.) Link <i>Ernodea littoralis</i> Sw. <i>Eustoma exaltatum</i> (L.) Griseb. <i>Galactia pinetorum</i> Small <i>Ipomoea pes-caprae</i> (L.) Sweet <i>Leptilon canadense</i> (L.) Britt. <i>Lithophila vermicularis</i> Uline <i>Metastelma Northropiae</i> Schlecht. <i>Panicum maximum</i> Jacq. <i>Paspalum caespitosum</i> Flugge <i>Smilax auriculata</i> Walt. <i>Spartina spartinae</i> (Trin.) Merr. <i>Syntherisma paniceum</i> (Sw.) Nash

Table 2. *Plant populations of the shrub and tree communities of the sand strand*

<i>Strand-scrub associates</i>	<i>Strand-hammock associates</i>
In order of frequency and constancy	In order of frequency and constancy
<i>Suriana maritima</i> L. <i>Lantana involucrata</i> L. <i>Guilandia crista</i> (L.) Small <i>Solanum bahamense</i> L. <i>Borrichia arborescens</i> (L.) DC. <i>Melanthera hastata</i> Michx. <i>Chamaesyce buxifolia</i> (Lam.) Small <i>Canavali lineata</i> (Thunb.) DC. <i>Calonyction tuba</i> (Schlecht.) Colla <i>Opuntia Dillenii</i> (Ker.) Haw. <i>Hymenocallis keyensis</i> Small <i>Uriola paniculata</i> L. <i>Andropogon scoparius</i> Michx. <i>Cyperus brunneus</i> Sw. <i>Flavaria linearis</i> Lag.	<i>Pithecolobium guadalupense</i> Chapm. <i>Jacquinia keyensis</i> Meg. <i>Coccothrinax jucunda</i> Sarg. <i>Metopium toxiferum</i> (L.) K. & U. <i>Reynosa septentrionalis</i> Urban <i>Capparis jamaicensis</i> Jacq. <i>Erithalis fruticosa</i> L. <i>Thrinax microcarpa</i> Sarg. <i>Conocarpus erecta</i> L. <i>Eugenia buxifolia</i> (Sw.) Willd. <i>Torrubia longifolia</i> Britt. <i>Gymnanthes lucida</i> Sw. <i>Coccolobis uvifera</i> (L.) Jacq. <i>Panicum divaricatum</i> L. <i>Smilax auriculata</i> Walt.
Additional species in alphabetical order	Additional species in alphabetical order
<i>Alternanthera maritima</i> St. Hil. <i>Ambrosia hispida</i> Pursh <i>Avicennia nitida</i> Jacq. <i>Batis maritima</i> L. <i>Chloris petraea</i> Swartz. <i>Coccolobis uvifera</i> (L.) Jacq. <i>Coccothrinax jucunda</i> Sarg. <i>Conocarpus erecta</i> L. <i>Dondia linearis</i> (Ell.) Millsp. <i>Ernodea littoralis</i> Sw. <i>Iva imbricata</i> Walt. <i>Metastelma Northropiae</i> Schlecht. <i>Smilax auriculata</i> Walt. <i>Tournefortia gnaphalodes</i> R. Br.	<i>Calonyction tuba</i> (Schlecht.) Colla <i>Capparis flexuosa</i> L. <i>Epidendrum tampense</i> Lindl. <i>Ernodea littoralis</i> Sw. <i>Eugenia axillaris</i> (Sw.) Willd. <i>Lantana involucrata</i> L. <i>Limonium carolinianum</i> (Walt.) Britt. <i>Maytenus phyllanthoides</i> Benth. <i>Metastelma Northropiae</i> Schlecht. <i>Opuntia Dillenii</i> (Ker.) Haw. <i>Osmia frustrata</i> (B. L. R.) Small <i>Pharbitis cathartica</i> (Poir.) Choisy <i>Rivina humilis</i> L. <i>Tillandsia aloifolia</i> Hook.

Table 3. *Flora of the rock hammocks*

<i>Boca Grande Key</i>	<i>Larger islands of Florida Keys near Key West</i>
In order of frequency and constancy	Commoner shrubs and trees in alphabetical order
Maytenus phyllanthoides Benth. Pithecolobium unguis-cati (L.) Benth. Cordia sebestena L. Torrubia longifolia Britt. Capparis flexuosa L. Thrinax parviflora Sw. Jacquinia keyensis Meg. Bumelia angustifolia Nutt. Borrchia arborescens (L.) DC. Dondia linearis (Ell.) Millsp. Opuntia Dillenii (Ker.) Haw. Eugenia axillaris (Sw.) Willd. Diapadium assurgens (L.) Kuntze Philoxerus vermicularis (L.) R. Br. Limonium carolinianum (Walt.) Britt. Capparis cynophallophora L. Gossypium hirsutum L. Rivina humilis L. Erithalis fruticosa L. Calonyction tuba (Schlecht.) Colla Acanthocereus floridanus Small Osmia frustrata (B. L. R.) Small Poinsettia pinetorum Small Yucca aloifolia L. Setaria macrosperma (S. & M.) Schum. Flavaria linearis Lag. Lycium carolinianum Walt. Elaphrium Simaruba (L.) Rose Solanum Blodgettii Chapm. Waltheria americana L. Galactia spiciformis T. & G. Sporobolus domingensis (Trin.) Kunth. Tillandsia aloifolia Hook. Epidendrum tampense Lindl. Achyranthes ramosissima (Mart.) Standl.	Acacia angustissima (Mill.) Kuntze Amyris elemifera L. Ananomis Simpsonii Small Bumelia angustifolia Nutt. Byrsonima lucida (Sw.) DC. Capparis flexuosa L. Carica papaya L. Casasia clusiifolia (Jacq.) Urban Citharexylum fruticosum L. Coccolobis laurifolia Jacq. Coccolobis uvifera (L.) Jacq. Coccothrinax jucunda Sarg. Conocarpus erecta L. Cordia sebestena L. Elaphrium Simaruba (L.) Rose Erithalis fruticosa L. Ernodea littoralis Sw. Erythrina arborea (Chapm.) Small Eugenia axillaris (Sw.) Willd. Eugenia buxifolia (Sw.) Willd. Ficus brevifolia Nutt. Ichthyomethia piscupila (L.) A. Hitchc. Jacquinia keyensis Meg. Lantana involucrata L. Lysiloma bahamensis Benth. Metopium toxiferum (L.) K. & U. Mimusops emarginata (L.) Britt. Morinda Roioe L. Pisonia aculeata L. Pithecolobium unguis-cati (L.) Benth. Randia aculeata L. Rapanea guyanensis Aubl. Reynosa septentrionalis Urban Sabal palmetto (Walt.) Todd Serenoa repens (Bartr.) Small Simarouba glauca DC. Solanum bahamense L. Thrinax microcarpa Sarg. Torrubia longifolia Britt. Ximenia americana L.

Life Forms

The different percentages of the life forms of the flora of these communities (table 4) are significant, particularly when compared with one another and with those found in similar habitats elsewhere. By the use of Raunkiaer's statistical methods of comparing the biological spectra of the islands with one another and with his "normal spectrum" (Raunkiaer, 1934, pp. 111-117, 178-189), a number of significant features are disclosed. The "plant climate" of these islands varies sufficiently, especially as regards precipitation, to show a definite difference between the spectra of Long

Table 4. *Life forms of plants of the strand communities*

Percentage distribution of the species among the life forms*

Associes	No. of species	S	E	M	N	Ch	H	G	Th
Strand-beach	18	...	...	...	9	36	18	9	27
Strand-dune	36	...	...	...	27	27	18	9	18
Strand-scrub	24	7	...	...	57	23	7	7	...
Strand-hammock	25	4	8	36	24	8	8	12	...

*Key to symbols for life forms: S, stem succulents; E, epiphytes; M, microphanerophytes; N, nanophanerophytes; Ch, chamaephytes; H, hemicryptophytes; G, geophytes; Th, therophytes.

Table 5. *Comparison between the life forms of strand plants of the Tortugas and those of other islands of the Sand Keys*

Percentage distribution of the species among the life forms*

	No. of species	S	E	M	N	Ch	H	G	Th
Tortugas Keys native species	35	6	...	...	22	18	15	6	33
Other islands	70	3.8	3.8	11	36.4	18.2	11	3.8	11

*See footnote to table 4.

Beach or Boca Grande Key and those of the Tortugas Keys, as given in table 5. Comparison of the spectra of the herbaceous strand communities with those of the shrub and tree communities gives a good idea of the differences in physiognomy. Dominance of chamaephytes and hemicryptophytes, with local and seasonal variations in the number of therophytes, is typical of strand-dune associes. Therophytes and rhizome geophytes are common in the strand-beach associes. Nanophanerophytes dominate the strand-scrub associes, and a well developed strand hammock is dominated by microphanerophytes, with some epiphytes present.

In a psammosere such as this one of the strand, therophytes, chamaephytes, and some rhizome geophytes are the pioneers, followed by hemicryptophytes and more chamaephytes, then by the ascending series of phanerophytes. On these islands the phanerophyte series is not well developed.

This brief study of life forms could be enlarged to show many more ways of using it as an index to the habitat and to the physiognomy and structure of the community, but such a study is reserved for a future paper.

Dispersal

There are a great number of pantropic genera and even species in the strand flora. Of these, *Ipomoea pes-caprae*, *Sesuvium portulacastrum*, and *Suriana maritima* are three of the commonest species. *Tournefortia*, *Chamaesyce*, *Canavali*, *Scaevola*, *Calonictyon*, and *Caesalpinia* are common genera. A majority of the strand species of these islands are common to all the West Indies.

The mangrove species of Florida are common to all the tropical Americas and the west coast of Africa. The genera *Rhizophora* and *Avicennia* are also found in the Orient, with many additional mangrove genera (Warming, 1925). The mode of dispersal of these mangroves has been described by Guppy (1917), Davis (1940), and others. In this Sand Key region many seedlings of *Rhizophora* were cast overboard from boats and recovered on the shores of the Tortugas islands. These experiments showed that the seedlings had no difficulty in migrating from east to west in this region. Other evidence showed that it is entirely probable that the other mangrove species can also float efficiently, and that no doubt all the mangroves are able to survive long voyages.

Less detailed observations have been made on the dispersal of some of the strand plants. Millspaugh (1907) gave in his "Distributional notes" and in his "Sequence of appearance" the probable mode of dispersal of some of the species. About some of these he was in error; for instance, he lists both *Avicennia* and *Laguncularia* as avevectent, whereas they, like *Rhizophora*, are transported almost entirely by water.

Land and water birds play an important part in the dispersal of the strand plants. Many of the fleshy-fruit plants, such as *Scaevola*, *Pithecolobium*, *Coccolobis*, *Solanum*, *Lantana*, *Jacquinia*, *Coccothrinax*, and *Opuntia*, may be eaten and their seeds thus transported by birds. Wading birds probably carry on their feet some of the commonest seeds, such as *Cenchrus*, *Cyperus*, *Chamaesyce*, *Andropogon*, and *Borrichia*. It is doubtful, however, whether as many seeds are thus carried as Millspaugh indicates.

Aquavection is the most efficient mode of dispersal, and accounts for the wide distribution of many of the pioneer strand plants. *Sesuvium*, *Cakile*, *Ambrosia*, *Canavali*, *Caesalpinia*, and other pod-bearing legumes, and probably *Tournefortia* and *Suriana* are transported by water.

The high winds common to this region may transport even heavy seeds, fruits, and other parts of plants. Small (1913) and others think that hurricanes have had much to do with the erratic distribution of many of the plants of the Florida Keys. Water-borne plants may be washed far inland

during storms, so that their distribution is not limited to areas near shore.

The list (table 7, p. 182) of cultivated plants and weeds of the Tortugas includes most of the species carried by man. Most of the weeds and some of the grasses were brought in on boats and are ballast plants. Such ornamental and fruit plants as *Thespesia*, *Cocos*, *Carica papaya*, *Ficus*, and *Agave* were planted. The latter and *Casuarina*, although originally planted, are now spreading by natural means.

A general conclusion is that most of the mangrove, salt-marsh, and strand-beach plants are aquavectent; the strand-dune plants are both aquavectent and avevectent; and most of the fruiting shrubs and trees of the strand scrub and strand hammock are avevectent. A much more detailed study of modes of dispersal of coastal plants is needed. These Sand Keys and the whole south Florida region derive their flora from all the Caribbean region. Guppy's (1917) study should be enlarged and brought up to date.

ENVIRONMENTAL FACTORS

Introduction

The two most important sets of environmental factors are the salinity of the soil water and of the surface water when present, and the physical and organic conditions that affect the water-holding capacity of the various soils. The climatic factors of temperature, rainfall, humidity, evaporating power of the air, wind, and intensity of light are fairly uniform and do not operate so effectively as the first two sets of factors in delimiting the plant communities. Rainfall affects the strand vegetation but has little or no effect on the mangrove vegetation, the roots of which are usually in water-soaked soils. All the plants are tropical or semitropical and cannot withstand hard frosts. The maritime factors, such as tides, prevailing winds, waves, and storms, are periodically and locally important. The tides are particularly important in the mangrove communities and the strand-beach associates of the fore dunes and upper beach.

In the mangrove swamps the most important factors are the water level, which is controlled by the tides and to some extent by the rainfall; the salinity of the surface and soil water; the physical and organic nature of the soils, and their depth and horizons; the rock or soil substrata below the sedimentary and organic soils; the aeration of the surface water and soils; and drainage from or into the swamps. Most of these were considered in some detail in the description of the ecology of mangroves (Davis, 1940). In general, the shore mangroves, mostly *Rhizophora* consociates and associates, are subject to an average tidal coverage of from 18 inches to 3 feet, and there is seldom much variation from the average salinity of 3.6 per cent. The soils are mostly sedimentary marl with some calcareous sand and a few

shell and rarely coral fragments. Peat and muck soils are locally abundant, especially toward the interior of the older swamps. The mangrove swamps toward the interior of the islands, which are sometimes not connected directly with the sea and not directly affected by the tides, normally grow on shallowly flooded soils. There is much variation in salinity, from about 5 per cent to less than 1 per cent. The areas are poorly drained and the water and soils poorly aerated. The soils of many of these mangrove flats are a thin covering directly over a limestone substratum. The mangrove and salt-marsh communities farthest inland are seldom if ever flooded. The soil or intermittent surface water may be over 9 per cent saline.

On the other hand, the strand communities are most affected by the porosity of the soils and their organic content, both of which control the water-holding capacity of the coarse calcareous soils common to the strand parts of these islands. The soil-water salinity is also very important, but it is very difficult to distinguish between the effects of salinity and of dryness. Both produce certain xeromorphic features in the plants, that can be attributed either to high salinity or to low soil water. The rainfall, wind, and sunlight all affect strand vegetation more than they do mangrove vegetation.

Thus we see that both types of vegetation are affected by salinity, and this salinity is usually tied in with soil water. The essential differences between the two habitats are the result of differences in elevation. In the swamps there is flooding of the soils, which are usually fine-particled, whereas in the case of the strand there is inconsistent flooding or none at all, and the soils are coarse.

Certain topographic features are naturally primary causes of the differences in some of the environmental factors. The elevation of the different parts of the sand plateau directly affects the water content of the soils. Low swales in the plateau often contain water after rains or storms. The higher, steeper dune terraces are often eroding away so rapidly that no plants survive on their faces and the roots of the plants on the crests are being exposed. The distance of the plants from the shore may affect growth, as those near the shore are more likely to be influenced by salt spray and high waves than those farther back, even if on equally elevated soils. The configuration of the island, that is, whether or not its main strand shore lies parallel to or across the direction of the prevailing winds, is important.

In this study, owing to lack of time, measurements of some of the differences in environmental factors could not be made, but the essential differences could be estimated by numerous observations. The following analyses of the details of some of these factors are based partly on measurements and partly on observations of the habitats of the strand communities.

Salinity and Soil Moisture

Samples of strand soils were weighed as quickly as practicable, then air dried and later oven dried and weighed. The percentage of soil water in relation to the dry weight was then calculated. Salinity was determined by grinding a 10-gram sample of air-dried soil, treating this with 100 cc. of sodium sulphate, filtering, then titrating a portion of this with silver nitrate, using potassium chromate as an indicator. The percentage of chloride in relation to the actual amount of soil water for that sample was then calculated. The expression of chloride in terms of percentage of the soil moisture gives a much better idea of the effective salinity than expression of chloride in terms of the total moist soil.

About fifty such samples were taken of the soils from the different strand communities of six of the islands: two at the Tortugas, two at the Marquesas, and two from the group near Key West.

The outer strand-beach associates is on the most moist and most saline soils, and great differences both in salinity and in soil moisture occur from place to place and time to time. The average soil water of the middle beach is below 12 per cent at low tide, and the soils near the water line are saturated at high tide. Since the time interval between tides is short, the plants with runners, stolons, rhizomes, and other types of underground stems are usually able to obtain ample water from the soils a few inches below the surface.

The soil-solution salinity of this outer zone of pioneer vegetation was found to be between 2 and 3 per cent, although the salinity of the sea water is above 3.5 per cent. This lower concentration of chloride in the upper-beach sands near the areas covered by the tide is probably due to dilution by rain water, which is common in the sands at the season of the investigation.

Inland from the upper beach toward the interior, the total soil water and salinity both decrease rapidly. At the Tortugas Keys, where the sand soils are coarsest, the percentage of soil water decreased from an average of 9.5 in the strand-beach associates zone to 5.5 in the *Uniola* strand-dune associates, to 4.7 in the *Suriana* consociates, to 3.8 in the *Chamaesyce* associates. But there is a great deal of variation in these percentages from place to place and season to season. On the two islands of the Marquesas group where samples were taken, the soil water decreased from 12 per cent on the upper beach to about 5 per cent in the strand-scrub associates and increased to more than 15 per cent in the strand hammock.

This increase of soil water in the strand-hammock soils is very significant. It is due to the increased humus content of the soils. This humus collects from the remains of previous vegetation and from seaweeds cast on the upper beach and fore dune and incorporated in the dune soils. It was not practicable to determine the percentage of this plant humus, but the

darker color of the top soils of the interior as compared with those of the open strand was readily noticeable.

Around ponds and in swales of the dune plateau the highest percentages of both soil water and salinity were found. Some consociates of *Sesuvium* and *Alternanthera* grow where the coarse soils are nearly saturated with water, over 20 per cent, and *Batis* and mangroves on the border between the strand and swamp grow where the salinity averages above 5 per cent.

Nature of Strand Soils

The calcareous matter forming the great proportion of the soil materials of the strand sands consists mostly of broken and angular parts of many plants and animals, so that the sands do not pack tightly, and their structure is loose and their texture coarse. This condition explains the relatively low water-holding capacity of these soils.

Also as a consequence of this type of soil, the beaches slope steeply and are narrow. The loose sands are easily shifted about by water. The dune terraces are steep. The sands are not easily blown about by wind to form high dunes. Percolation of water through the soil is rapid and the surface dries quickly. After a rain, or between the tides, the top soil dries very rapidly. The calcareous particles retain a surface, hygroscopic film of water and perhaps some combined water, which can only be driven off at high temperatures and which is of no use to the plants. Root penetration is easy and most of the plants have deep roots, reaching well below the dry top soils. There are such long spells without rain, however, that the soils probably become dry as deep as the water table.

The beaches accumulate abundant seaweeds, such as *Sargassum*, *Thalassia*, *Cymodocea*, and algae, especially *Falimedia*, with a few animal remains. Such organic debris begins the addition of humus to the calcareous sands. The strand plants add to this humus, and movement of the sand mixes these organic materials with it. As the sands become stabilized, this humus forms an upper horizon that is the most important factor in retaining more soil moisture, thus enabling mesophytes to replace xerophytes to form a hammock forest.

There seems to be a gradual increase in particle size of the sands from Key West westward. Certainly at the Tortugas the sands are coarsest, because of the abundance of parts of coral, especially on some of the low islands.

Rainfall and Temperature

The mean annual rainfall decreases regularly westward from over 60 inches at Miami, to 42 inches at Long Key, 38 inches at Key West, and about 33 inches at the Dry Tortugas. The few records for the Tortugas are far from complete, but the Key West records cover a long period, over 70 years. All

the records for the Florida Keys show two definite six-month periods: a dry season from November through April, and a wet season from May through October. At Key West the wet season averages 28 inches rainfall, whereas the dry season averages less than 10 inches.

This long dry season is the most critical factor of the climate of these islands. In some instances there has been less than $\frac{1}{2}$ inch of rainfall during two months. In 1937-1938 there was less than 2 inches of rainfall at the Tortugas from December through March. This seasonally arid condition is accentuated by the coarseness of the calcareous sands and is reflected in the vegetation.

It is easy to recognize the increasingly mesic conditions of the strand when a comparison of vegetation is made on the islands from the Tortugas eastward along the Florida Keys. The paucity of rain no doubt helps to account for the lack of hammock plants at the Tortugas Keys, since enough humus has accumulated at a number of places for the development of a more mesic vegetation. Although, because of lack of data, direct correlations between the vegetation and the rainfall cannot be made, such a correlation seems to be clearly indicated. A gradual decrease in rainfall westward, and a gradual increase in coarseness of the sands, both contribute to the gradual decrease in mesic plant communities.

The temperature is much less significant, as there is little variation along the Florida Keys. Miami has a mean annual temperature only 2° F. lower than that of Key West, but may occasionally suffer from light frosts, which have never been recorded at Key West. The Sand Keys region is without any violent fluctuations in temperature. At Key West the mean high temperature is from 75 to 88° F. for the year, and the mean low is from 65 to 78° F. The lowest records are for only a few days and are about 40° F. Therefore the vegetation is seldom if ever affected by low temperatures, and the average condition is about that of the tropics.

Wind, Storms, and Light

These three environmental factors, ordinarily of minor importance in most habitats, are unusually effective here. Nearly constant winds, occasional severe storms, and intensive sunlight, particularly on the strand, are characteristic of tropical shores. These islands are especially exposed to all three of these conditions.

The effect of prevailing winds is very noticeable because it produces asymmetrical growth forms in some of the plants; and by evaporation tends to produce many xeromorphisms, discussed below. The flat-topped, one-sided growth form of many dune plants, particularly *Tournefortia* (see pl. 2, fig. 1), has been noted and discussed by many observers. Wells and Shunk (1938) stress the effects of salt spray in causing limb pruning in such plants, and consider the wind not the only cause. This growth form, however, oc-

curs far in the interior, on high mountains, and has been described as a "Krummholz" type of vegetation. Like Doult (1941) and many others, the author thinks that the limb pruning and asymmetrical growth are almost if not entirely due to wind, salt spray playing only a minor role.

Winds and storms do have the effect of sending salt spray far to the interior. A number of leaves of plants over 200 yards from the beach were washed after a moderate windstorm, and a titration of the water with silver nitrate showed the presence of chloride. The salinity of soils away from the direct spray of the beaches is increased by storms.

The action of wind on a few woody plants to produce changes in growth form, and the occasional carrying of salt spray far to the interior, are much less important than the effects of wind, with high temperature, on the rate of transpiration. The evaporating power of the air was measured at a number of places by Livingston porous-cup atmometers, and the rate of evaporation per day was found to average 30.1 cc. near the beach, 28.5 in the strand scrub, and 20.6 in the more protected mangrove swamps, for two periods of 15 days each. This relatively high rate of evaporation increases the xeric conditions of the strand and, with the low water content of the coarse strand soils, produces extremely dry habitat conditions. These islands have more constant winds than those farther north, because they are longer in the trade-wind zone and are more exposed.

Storms, some of great violence, affect the topography as well as the vegetation of these islands. In the detailed descriptions of the islands, below, many instances of changes produced by storms are cited. Tropical hurricanes are most effective in causing changes in the strand sands and the strand plants; the mangrove swamps are best able to withstand them. Storms are also effective in the dispersal of some of the plants, blowing the seeds and other parts great distances and causing some of the erratic distribution of the flora on the Florida Keys. The storms wash salt water far into the interior and completely over many of these islands, in some cases killing all the vegetation. There are a few or no islands of this group that have not been in some way denuded or partly denuded of vegetation over a long period of years. It was impossible to find accounts of many of these storms, but in some instances such accounts described the shifting of the sands, the breaking and uprooting of the vegetation, and the killing of many of the plants by submergence and increase in salinity.

The intense sunlight, both from above and reflected from the sands, has an effect on the vegetation. The amount of this light was not accurately measured, but some idea of it was gained through the use of a Weston light meter, carried for photography. The quantity of light reflected from the sands is almost as great as that from the sky in some places. Light decreased markedly in the interior of a close growth of strand scrub or strand-hammock forest, but elsewhere the vegetation casts little shade.

This intense light has its effect, together with high temperatures and wind, in increasing the loss of water from the plants. The light form of some plants, as *Ipomoea pes-caprae*, is distinctly different from the shade form, being much more xeromorphic.

Elevation, Inundation, Erosion, and Accretion

A consideration of environmental factors would be incomplete without reference to these physiographic processes. They are much the most important of the factors producing many of the differences outlined above. As already pointed out, differences of a few inches in elevation of the soil and of a few inches in depth of inundation by the tide account for the essential features of the habitats of the strand and mangrove communities. In general, the average coverage by water of any of the zones of the mangrove swamps, and the average elevation of any of the zones of the strand vegetation, are fairly constant from island to island. Changes in elevation of the mangrove soils that lessen the depth of inundation produce changes in the mangrove forest. Likewise, increases in elevation of the strand soils lead to gradual changes in the strand vegetation. None of the islands have soils above about 9 feet, and few of the mangrove swamps grow in water over 2 feet deep at mean tide, so that the little difference of about 11 feet in elevation among these islands accounts for most of the differences in vegetation.

Erosion resulting from changes in direction or intensity of the currents, tides, and winds, and from severe storms, may slowly or rapidly affect the topography and the vegetation. In the case of storms, many low sand areas are completely washed away or shifted about. The muds of the swamps are most easily shifted by changes in the currents and in the tidal flow or ebb. The steep terraces leading up from many of the beaches to the more elevated dune plateaus are mostly the results of wave action during mild or heavy winds. New gaps between islands have been cut by storms, changes in currents, and the gradual shifting of strand soils.

Accretion similarly effects changes in topography and consequently in vegetation. The gradual accretion of marl, muck, and peat soils in mangrove swamps has been discussed. Many of these islands are the direct result of such accretions. Over the mud and peat soils built up by the mangroves, sand soils often migrate. In general, the accretion of sand soils is much more rapid and most directly affects the plant communities. As the upper beach builds up dunes, these are shifted to higher levels or farther inland. As vegetation increases, these sands become more or less fixed, accretion is slowed down, and topographic and vegetation changes are less directly due to the results of accretion. These coarse sands do not pile up into high dunes, and elevation of soil above about 4 feet is slow and only occasional. The sands do, however, readily shift about on the beach

and in the sea currents, causing rapid changes in the beach line, bare spits, bars, and other formations. On these newly formed sands, plants of the strand-beach associates quickly begin the vegetational succession.

ADAPTATIONS AND XEROMORPHISM

The distinctive adaptations of the plants of the strand, salt marshes, and mangrove swamps to xeric and halic conditions are notable. The most obvious of these adaptations consist in form and structural features of the leaves, most definitely related to conservation of water in the tissues. The general term applied to such modification is xeromorphism. Xeromorphism in mangrove, salt-marsh, and other plants of saline habitats has long been considered an expression of the plants' reaction to the "physiological dryness" of these wet habitats. The striking similarity of the adaptations of many strand plants to those of salt-marsh or mangrove plants serves to emphasize the probable lack of available water in both the dry strand soils and the wet marsh and swamp soils. Here on these islands the habitats and plants both offer a fine opportunity to correlate the development of xeromorphism with environmental factors. A number of observations and some anatomical studies of structure were made to aid in determining the most significant adaptations.

In brief, the environmental factors most conducive to xeromorphism are: (1) soil-water salinity, (2) coarse sand soils that retain little water, (3) strong and almost constant winds, (4) comparatively high temperatures, and (5) intense illumination from above and reflection from the sands. The most obvious adaptations are of the leaves, for example, change in position during the day, reduction in size, hairiness, succulence, thickened cuticle and epidermis, sunken stomata, and other features. Most of these adaptations reduce transpiration and some aid in water storage. Some of the plants have many of these features and others only one or a few. The adaptations of some of the most typical plants of the strand and a few of the mangrove and salt marsh are summarized in table 6.

Keinholz (1926) in his study of the Philippine beach plants, and Harshberger (1908) in his study of Bermuda dune plants, both made more detailed studies of these adaptations. Some information gained from them is included here.

In the table a number of species with different forms are noted. These are in some instances very strikingly due to differences in habitat, but in other instances they seem to be entirely genetic. Thus, there are distinct shade and sun forms of *Ipomoea pes-caprae*, and *Conocarpus erecta* has a thick, succulent leaf form on the most exposed stems and a thinner form on the more protected stems. In *Ipomoea* the shade-form leaf is half or a third as thick as the sun form, and has little or no water-storage tissue and no lower palisade. In *Conocarpus*, besides the two leaf forms of *C.*

erecta there is a silky-leaved variety, *sericius*, that seems definitely genetic. Similarly *Borrichia arborescens* has two forms, one hairy and the other smooth. Some taxonomists distinguish the two forms as distinct species. They may be entirely genetic, as no definite correlation between habitat and either of the two forms could be noted.

Bowman (1917) in his study of the red mangrove, and the author in similar anatomical studies of mangrove leaves of all species, have found that in *Rhizophora*, *Laguncularia*, and to a much less extent *Avicennia*, an in-

Table 6. Summary of some of the structural adaptations of the leaves of certain strand, salt-marsh, and mangrove plants

Type of adaptation	Typical species with these adaptations
Change of position	<i>Ipomoea pes-caprae</i> , <i>Canavali lineata</i> , <i>Chamaesyce buxifolia</i>
Hairiness	<i>Tournefortia gnaphalodes</i> , <i>Lantana involucrata</i> , <i>Borrichia arborescens</i> (hairy form), <i>Conocarpus erecta</i> var. <i>sericius</i> , <i>Capparis jamaicensis</i> , <i>Gossypium hirsutum</i>
Succulence	<i>Sesuvium portulacastrum</i> , <i>Cakile lanceolata</i> , <i>Scaevola plumeri</i> , <i>Ipomoea pes-caprae</i> (sun form), <i>Tournefortia gnaphalodes</i> , <i>Iva imbricata</i> , <i>Conocarpus erecta</i> , <i>Laguncularia racemosa</i> , <i>Maytenus phyllanthoides</i> , <i>Batis maritima</i> (succulent stems: <i>Salicornia perennis</i> , <i>Opuntia</i> spp.)
Thick cuticle, thick epidermis ..	<i>Scaevola plumeri</i> , <i>Ipomoea pes-caprae</i> , <i>Conocarpus erecta</i> (thin-leaf form), <i>Rhizophora mangle</i> , <i>Canavali lineata</i> , <i>Cakile lanceolata</i> , <i>Borrichia arborescens</i> (smooth form), most of the grasses, the palms
Sunken stomata	<i>Ipomoea pes-caprae</i> , <i>Scaevola plumeri</i> , <i>Sesuvium portulacastrum</i> , <i>Lantana involucrata</i> , <i>Conocarpus erecta</i> , <i>Rhizophora mangle</i> , <i>Laguncularia racemosa</i> , <i>Borrichia arborescens</i> (smooth form)

crease in thickness particularly due to increase in water-storage hypodermis occurs in the leaves of plants grown in salt water of high concentrations as compared with those grown in water of low salt concentration or fresh water. The more shaded leaves are thinner than the more exposed. *Batis* and *Salicornia*, salt-marsh plants, have succulent leaves and stems respectively, the tissues being filled with a salty sap.

The similarity between some of these succulent salt-marsh and mangrove plants and the succulents of the strand-beach and strand-dune communities, and the usual presence of some salt in the soil water of the upper beach and dunes, makes it difficult to determine which factor, salinity or dryness, produces this xeromorphism. The fact that many of the strand species are normally associated with some salinity of the soil water but can grow in almost nonsaline situations, as they do on the top of Fort Jefferson, indicates that succulence and other adaptations of strand plants are prob-

ably due mostly to xeric conditions and little if at all to halic conditions.

Some strand plants and most of the mangroves have been considered halophytes. The former are facultative halophytes, but for the most part simply xerophytes with little need for salt. In the case of the mangroves, many plants of all three species in Florida have been grown without difficulty for from 3 to 5 years in salt-free soils and water, a fact which indicates that they are not obligatory halophytes. No doubt further studies would show that the habitat preference of many of these strand and mangrove plants may be for some salinity, but that they are facultative to many different degrees of salinity. The essential inference here is that both halic and xeric conditions may produce the typical modifications of xeromorphism. It is almost impossible to state which factor, dryness or saltiness, produces the particular adaptation.

PART II. DETAILS OF THE ISLANDS

THE GROUP NEAR KEY WEST

Topography

Boca Grande Key, Man Key 1.2 miles east of it, Ballast Key 750 feet farther east, the group composing the Woman Keys 2 miles still farther east, and Crayfish Key 2 miles still farther east form the southernmost chain of islands of the group near Key West (see fig. 1, p. 121). All are formed on the dissected southern rim of the oölite limestone bank described above (see "Location, topography, and geology"). All but the small Crayfish Key have sand beaches and plateaus as well as flooded mangrove-swamp areas. Barracuda Key, about 3000 feet north of the Woman Keys, and these southernmost islands were the only ones studied in any detail.

There has been a certain amount of confusion regarding the names of Man Key and the Woman Keys. United States Coast and Geodetic Survey chart 584 names the island nearest Boca Grande Key, Woman Key. Millspaugh names it Man Key, and local fisherfolk use no consistent name. The oldest authority found was a military map by Lieutenant J. C. Ives, of April 1856, which names it Man Key. Therefore the island nearest Boca Grande Key is here considered Man Key, and the group of islands farther east, south of Barracuda Key, are the Woman Keys, or Woman Key. The plural is used here because, although the island was in one main piece before Lansing's surveys, it has been in two parts for a long time.

The probable mode of formation of the southernmost row of islands, by differential erosion of the limestone bank, has been outlined above. Boca Grande Key, the largest, was left with a large area of exposed oölite rock, and Man Key has some of this rock exposed at low tide in the lagoon that penetrates its center from its western end. This rock also appears around the southern end of Ballast Key and in the shallows south of the eastern part of the Woman Keys. The beaches, sand plateaus, and inundated marl-mud areas of each of these islands have probably built up around and over the elevated rock areas. The islands all differ in size and shape and in the relative areas of sand and mud. Ballast Key has no marl areas except mud accumulated in a nearly filled-up pond. Barracuda Key is nearly all of low elevation, with only narrow sand ridges around parts of a ponded interior.

The two Mullet Keys, Cottrell Key, the Archer Keys, Mule Key, and Crayfish Key are all completely or almost completely inundated by the tides. We shall not consider any of these in detail.

Boca Grande Key

Topography. Boca Grande Key is the largest island of the group near Key West. It is also the only island of the Sand Keys with large areas of rock

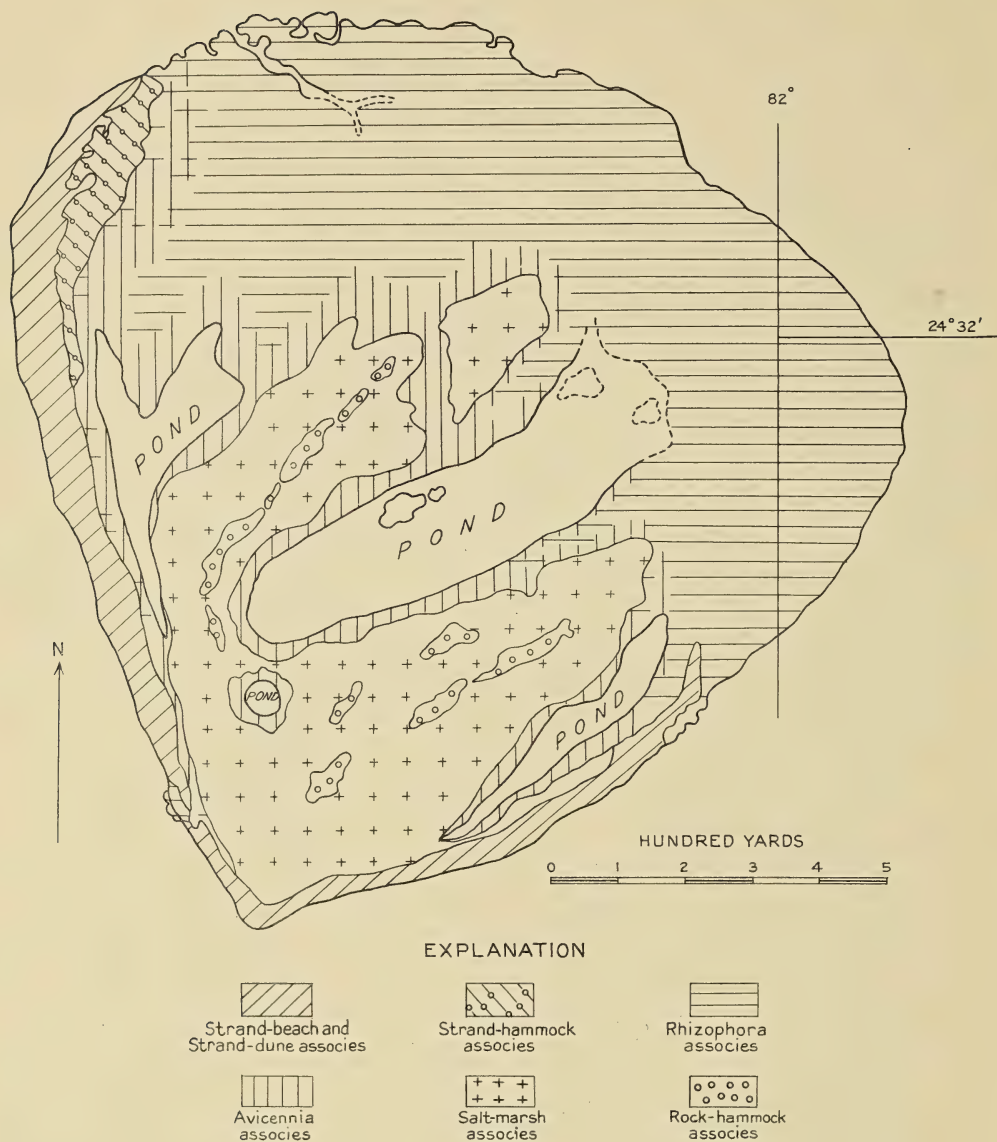


Fig. 3. Boca Grande Key

exposed at the surface. It may, therefore, be considered as probably the oldest and most permanent island of the Sand Keys. The rock shelf of which its central part is composed is an elevated part of the underlying oölite limestone rock. The present Boca Grande Key consists mainly of calcareous sands and mangrove-swamp muds accumulated around this central rock plateau. The sands have accumulated on the west and south sides, and muds, muck, and peat in mangrove swamps on the north and east sides. Lansing was entirely

mistaken in referring to the rock plateau as "consisting principally of small bits of coral rock."

Since this island is built on and around oölite lime rock, it probably has not changed much in either shape or elevation. The government charts and maps indicate little change during the past 75 years. Some parts of the southern and western beaches seem to have eroded away and later been extended from time to time. At present the shoal area around the southwestern tip shows signs of aggradation. The mangrove areas of the north and east sides are gradually extending out into the shoal water which surrounds the island on those sides. The deep Boca Grande Channel, to the west, cuts near the northwestern shore and prevents any extension in that part of the island.

At present (fig. 3) a narrow sand plateau of about 4 feet elevation extends around about half of the island from its northern border along all its western border and more than half its southern border. A narrow beach extends around nearly all of this sand-dune plateau. There is usually a steep terrace from the beach to the dune plateau.

Inland from the sand-dune plateau is a large rock plain of low relief, with three large, shallow depressions covered by ponded water only partly or not at all affected by the tide. The highest parts of the rock plain extend in a U shape around the largest of these ponds. Over the lower, flooded parts of the plain, bordering and covering parts of the ponded areas, are mangrove flats. Over the intermediate parts of the plain, between the flooded and highest parts, the rock is bare or only thinly covered with soil. This rocky area supports a salt-water marsh associates.

The tide-flooded parts of the island include most of the northern and eastern and part of the southern areas. The mangrove swamps of this part were difficult to survey and their boundary is not well known.

The border between the dune plateau and the inland rock plain or the mangrove swamps is usually a steep terrace 2 to 4 feet high. As the dune sands are carried slowly farther inland, this inner terrace face of the sand strand is moving over the swamps and rock plain. This extension of the sand strand inland seems, however, to be very slow.

Most of the topographic features of this island are similar to those of the larger islands of the oölite limestone keys near Key West. A central rock plain, a shore-border sand plateau and beach, and tidal-flat mangrove swamps are three chief features of many of the Florida Keys. Thus Boca Grande is the only island of the Sand Keys that furnishes a good example of conditions prevalent on most of the other large islands of the western Florida Keys.

Vegetation. The central rock plain of this island has a rock-hammock associates and a salt-marsh associates, neither of which is found on the other islands, because the latter do not have rock plains. Some marl soils and

sandy marl soils such as encourage the development of hammock forests do exist on some of the other islands, but not over areas of sufficient height above the tide to form even a scrub hammock growth. The rock hammocks and the salt marshes found here are, therefore, unique among these small islands, although they are very common on the larger islands of the Florida Keys east of Key West.

The strand communities are well developed on the beach and the strand-dune plateau. The mangrove swamps are fairly well differentiated into distinct *Rhizophora* associates and *Avicennia* associates. *Conocarpus* occurs with some of the strand-hammock plants or simply as individuals along the border between the swamps and the strand. *Laëuncularia* also grows in the border zone and frequently is abundant in the mature *Rhizophora* associates of the swamps. A few of all three mangroves are to be found along some parts of the beach side of the island, growing on the lower beach and out into shallow water offshore.

The rock-hammock associates (pl. 2, fig. 2) is distinct although there is much similarity of species between it and the strand hammock; see tables 2 and 3. *Pithecolobium unguis-cati*, *Maytenus phyllanthoides*, *Opuntia* spp., *Thrinax parviflora*, *Bumelia angustifolia*, *Capparis flexuosa*, *Cordia sebestena*, and the epiphytes *Tillandsia aloifolia* and *Epidendrum tampense* (pl. 4, fig. 1) are fairly distinctive of the rock hammocks. Some of these species and many more are found in the hammocks of the larger Florida Keys near Key West; see table 3.

The difference in soils mainly accounts for the difference in vegetation between the sand and rock hammocks. Rock hammocks are on thin marl soil with abundant humus, whereas strand hammocks are on deep sand soils. Both are somewhat mesic, but the rock hammock more so. On Boca Grande Key, however, the marl soil is so thin over the rock that good conditions for growth of a hammock do not exist and the rock hammock is poorly developed. The plants are scrubby and many of them are dead or dying. Salt water from high tides and storms covers the area and causes death or retardation of some of the plants. The workers of the U. S. Plant Quarantine Service have eradicated nearly all the wild cotton, *Gossypium hirsutum*, from the area, and fires set by them or other persons have burned out many of the shrubs and trees. Millspaugh's account indicates a more thickly spaced growth than exists at present.

Around the small groups of trees and shrubs that form the scrubby hammocks grows a salt-marsh associates of a number of low shrubs and herbs, extending over the rock plain to the *Avicennia* trees and bushes which grow around the ponds. Between the normally flooded shores of the ponds and the parts sporadically flooded by rain, tide, or storm waters there is a zone nearly destitute of any plant cover. Much of this zone is bare rock broken

and eroded to form a rough plain (pl. 2, fig. 2). Patches of *Salicornia verennis* (pl. 3, fig. 2) and *Monanthochloe littoralis* cover some few parts of the area. Evaporation of water and consequent concentration of salt make the thin soils very salty; on some of these low, flat places the soil solution is over 10 per cent saline. On less salty, deeper, and more elevated soils, both the above plants cover large areas, and *Batis maritima* becomes abundant. *Batis* also grows abundantly with *Avicennia* in the flooded ponds. These three salt-marsh plants form fairly distinct zonal facies of the salt-marsh associates over the lower parts of the rocky plain.

At intermediate elevations of the rocky plain around and between the plants of the rock-hammock associates grows a varied assemblage of plants forming another facies of the salt-marsh associates. The most frequent and constant species of this associates on Boca Grande Key are *Sesuvium portulacastrum*, *Dondia linearis*, *Borrchia arborescens*, *Limonium carolinianum*, *Flavaria lineata*, *Melanthera nivea*, *Osmia frustrata*, and *Sporobolus dominicensis*. Small bushes, *Maytenus*, *Gossypium*, *Cordia*, and other shrubs, grow among these plants. There is not as sharp a line of demarcation between the marsh and hammock as is indicated on the map (fig. 3).

The strand communities, with the exception of the strand-beach associates, are well developed. Because of a very narrow beach and an abrupt rise of 3 to 4 feet to the dune plateau, the few typical strand-beach plants just above the wave line are widely scattered as individuals or in small colonies. *Cakile*, *Sesuvium*, *Cenchrus*, and a few individuals of *Tournefortia* are the commonest plants on the upper beach or on the edge of the outer face of the plateau.

The long dune plateau, extending over a mile along the western and southern shore of the island, averages about 60 yards wide and is of about 4 feet elevation. *Uniola paniculata* dominates the whole length of this strand-dune associates. With it are associated most of the species listed in table 1. Some of the most frequent and constant of these are *Chamaesyce*, *Waltheria*, *Andropogon heteroflorus*, *Canavali*, *Flavaria*, and *Hymenocallis*. Patches of *Suriana* occur.

Near the northwest end of the island the strand plateau widens out, and over the interior of this wider part a strand-hammock associates appears. This is not so well developed here as on some of the Marquesas Keys, but it is the only one on the islands near Key West. The commonest trees and shrubs of this strand-hammock associates are *Jacquinia keyensis*, *Pithecolobium guadalupense*, *Capparis jamaicensis*, *Metopium toxiferum*, *Conocarpus erecta*, and *Suriana maritima*. The abundance of the latter and the presence of *Solanum* and *Lantana* are indicative of conditions similar to those in the strand-scrub associates, which is the highest development of strand vegetation on the other islands of the group near Key West. The small size of

the hammock plants and the small number of species present clearly indicate that this associates is poorly developed and not nearly so mesic as a similar community on Long Beach Key.

The border between the strand plateau and the mangrove swamps, ponds, or salt-marsh flats is abrupt. Along that part where large mangroves shade the sand dunes, *Hymenocallis* and *Sesuvium* are abundant down to the water level, where *Batis* becomes a dominant under-story plant beneath the mangroves.

The extensive mangrove swamps are composed in the main of two communities, the mature *Rhizophora* consociates and an *Avicennia* salt-marsh associates. Neither of these is exactly similar to the community of the same name described by the author (1940), for the part of the swamp dominated by *Rhizophora* contains many *Laguncularia* and some *Avicennia*, so that it might better be termed an associates, and the *Avicennia* parts of the swamp have few or no salt-marsh plants, *Batis* only occasionally covering local areas.

Man Key

Topography. This is a long island, 4200 feet, with a narrow beach and dune area along its whole southern side. At the eastern end there is a bare sandy hook. Only a shallow channel separates it from Ballast Key, but there is no record that the two were ever joined. See figure 4.

The beach and dune area is narrow, widest at its eastern end, about 250 feet, and averaging only 150 feet along most of the southern front. The dune plateau averages from 3 to 4 feet high, and a steep dune terrace extends along most of the beach.

Back of the dune plateau is a broad, inundated part, average width 750 feet, into which a lagoon 1500 feet long (pl. 1, fig. 1) extends from the northwestern edge of the island. Small islets of mangroves grow in this lagoon on or about some of the lime rock exposed at high tide. Large flat areas extend over much of the interior. About three-fourths of the island is swamp and one-fourth strand.

Vegetation. The vegetation is distinctly zoned. The long beach is narrow, with only a few patches of the plants of the pioneer strand-beach associates on the dune terrace or upper beach. The dune plateau is also narrow, and is completely covered, except at the eastern end, by the strand-dune associates, with *Uniola*, *Canavali*, *Andropogon*, *Flavaria*, *Hymenocallis*, and *Bradburya* some of the most frequent and constant plants. A small group of shrubs at the eastern end includes some fairly large *Pithecolobium guadalupense* bushes, and a strand hammock has begun to develop.

There is a distinct belt of black mangroves, *Avicennia nitida*, between the dune plateau and the lowest parts of the key, which are covered almost entirely by a large red mangrove swamp. There is one large area in the

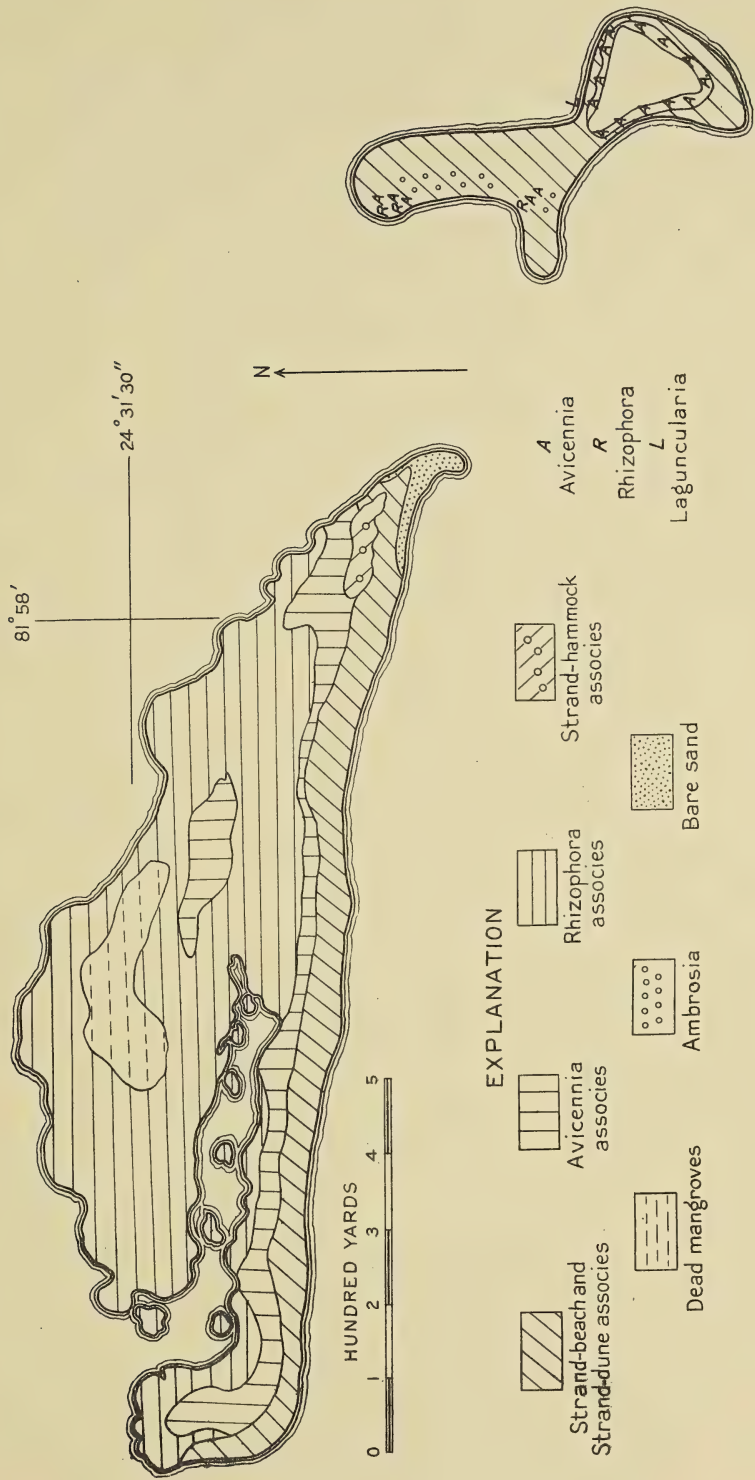


Fig. 4. Van Key and Ballast Key

interior of the red mangrove forest given over to *Avicennia*. A few *Laguncularia* trees grow with the black and red mangroves. The shore parts of the swamp are of large *Rhizophora* trees, but there are large areas in the interior covered by a growth of low red mangrove bushes.

The narrowness of the strand-dune area, the nearly complete absence of strand-scrub and strand-hammock plants, and the large areas covered by the mangrove-swamp communities are distinctive features of this island. Peat is accumulating in the swamp, but the sand areas are either young or not being built up very rapidly.

Ballast Key

Topography. Ballast Key (fig. 4) is small, oddly shaped, almost completely built of sand, and considerably changed since it was described by Millspaugh. There are now 750 feet of water between Man and Ballast keys, whereas Millspaugh reported that "this small key is separated from Man Key by a channel so narrow that the branches of the mangroves of both nearly touch." The present wide gap between the two seems to be due to the erosion of a small part of the western side of Ballast Key and a larger part of the eastern end of Man Key; that is, if the black mangrove pond shown by Millspaugh was located where a dried pond with fringing black mangroves now occurs. Also this island has increased a great deal in size if Millspaugh's measurements were anywhere near correct. He considered the area of the island to be less than $1\frac{1}{2}$ acres, whereas it is now about 10 acres. It seems entirely probable that the measurements given by Millspaugh in feet should have been given in yards. If this correction is made, the area figures are more nearly comparable. Some of the western part of the island has been eroded, leaving a steep wave-cut terrace, and the northern prong of the island has been extended.

The present island is a sand plateau with many parts 4 feet high, except for a dried-up pond in the southern triangular part of the island, a gently sloping beach along its eastern side, and a low shore with mangroves along the northwest point, extending into the shoal area near by. The average elevation of the sand plateau seems certainly to have increased since 1904, and the changes in shape indicate a shift of the island toward the north. The southern part of this island is the part described by Millspaugh, the northern part being more recent.

Vegetation. With the exception of the triangular dry pond and fringing *Avicennia* near the southern end, the colony of shore mangroves at the northwestern end, and a few mangrove bushes in a swale on the western side, the whole island is a strand-dune associates with a few strand-beach plants on the upper part of the gently sloping beach. This strand-dune associates is particularly notable because of the almost complete absence of *Chamaesyce*, the presence of large patches of *Ambrosia hispida* on the highest,

driest parts, and the relative abundance of *Tournefortia* near or on the dune terrace.

Both *Batis* and *Borrichia* form colonies near the dried pond, and grow among the few black mangroves that now remain around it. Stumps of *Avicennia* and an accumulation of peat and muck in the pond attest the former existence of a larger swamp there. All three mangroves grow on the extending shore at the northwest end of the island, and *Dondia* is associated with them.

A number of coconut palms have been planted in recent years around the edge of the strand plateau on the southern and eastern shores. This island is owned by Mr. N. B. Thompson, of Key West, and may be further planted with fruit or ornamental plants.

Woman Keys

Topography. The two largest parts of this group of islands and mangrove islets (fig. 5) are the eastern and western parts, now separated by a shallow but swiftly flowing 300-foot channel. This passage was there in 1904 but was very narrow. A storm in 1909 widened the passage, but it is now being closed again by the growth of a number of red mangrove colonies. The length of the eastern part is now 1650 feet along its southern shore, and its average width is about 600 feet. The length of the western part is 1850 feet along its southern shore, and its average width is 750 feet. The former has a beach and strand-dune plateau along its whole southern and most of its eastern shore, whereas the latter has only a small area of beach and open strand at its southeastern end, and nearly its whole southern shore is fringed by mangroves, back of which is a sand-plateau ridge. This long sand ridge was not noted by Millspaugh, and he thought that nearly the whole island was a mangrove swamp; but no doubt the ridge existed then and was hidden from view by the fringing mangroves.

Back of both the open sand plateau on the eastern part and the enclosed sand ridge on the western part are large inundated swamps. A shallow lagoon covers part of the eastern part. A fairly large mangrove colony forms an islet about 450 feet in diameter lying 150 feet north of the western part, to which it may soon become joined. This mangrove islet has been named by some persons Boy Key.

Vegetation. The eastern part has such a narrow beach that few communities or individuals of the strand-beach associates exist there. The strand plateau is very low, seldom over 2 feet above the tide, and its vegetation is an uncommon variant of the usual strand-dune associates, for here there is less than 5 per cent coverage by *Uniola*. *Spartina patens* and *Andropogon* sp. dominate the community. More community groups dominated by *Sesuvium*, *Borrichia*, *Dondia*, and *Batis* occur than is usually the case. The paucity of *Uniola* and the abundance of *Spartina* and other more halophytic plants,

especially in the depressions of the plateau, may be due to the general low elevation of this strand area.

Around the eastern end of the island there are a few scattered thickets of *Suriana*, *Pithecolobium*, and *Solanum*, forming an incipient strand scrub. There is also a group of the silky-leaved variety of buttonwood, *Conocarpus erecta* var. *sericius*; this is one of only two locations on these islands

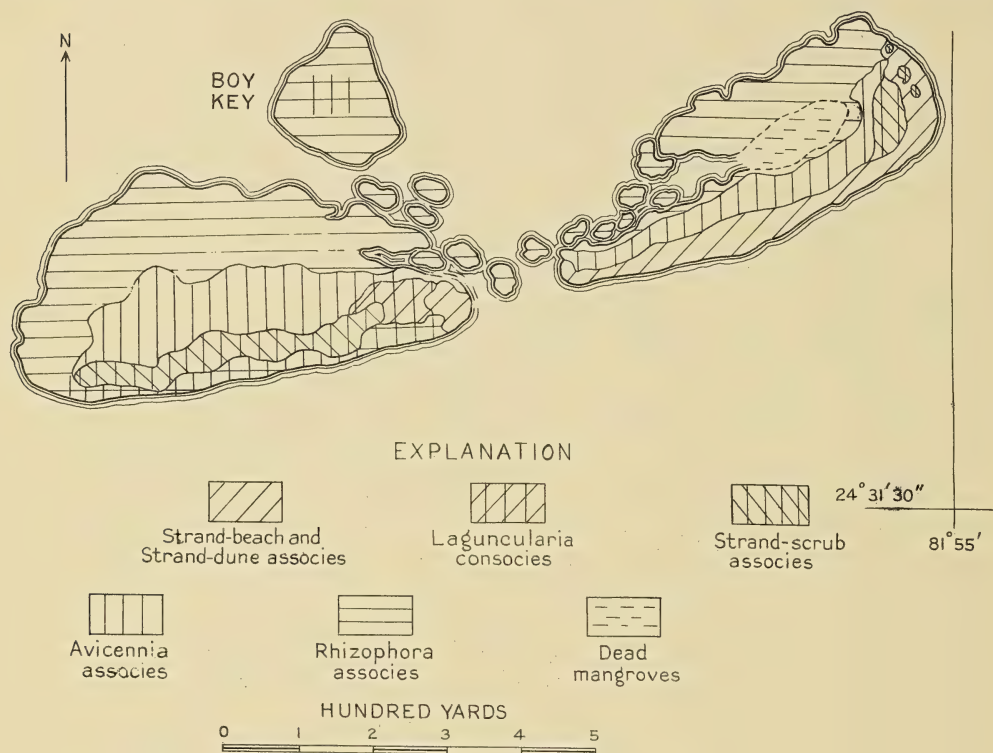


Fig. 5. Woman Keys

where this variety grows naturally, the trees at Garden Key having probably been planted there.

The mangrove-swamp area is distinctly zoned, with the *Avicennia* associes zone on the higher parts and *Rhizophora* over the most submerged parts. *Batis* is common in the *Avicennia* associes on the soils not normally tide-covered between the strand dune and the flooded mangrove flats.

The west part of the Woman Keys has only a small beach area at the eastern end, around a shack built there by rum runners. This low strand supports a few of the strand-beach and strand-dune plants. Along the other part of the southern shore a well developed mixed growth of *Rhizophora*, *Avicennia*, and *Laguncularia*, with *Conocarpus* on the slopes of the sand

ridge, forms a shore-fringe mangrove associates. On the long sand ridge back of this mangrove fringe has developed a thicket growth of shrubs and coarse grasses to form one of the best of the strand-scrub associates found on these islands. *Solanum*, *Guilandia*, *Lantana*, *Erithalis*, *Suriana*, and *Borreria* are the most frequent shrubs; *Rivina*, *Hymenocallis*, *Flavaria*, *Melanthera*, *Calonyction*, *Canavali*, *Cyperus*, *Chloris*, and *Panicum amarulum* aid in forming the scrub associates. A few *Conocarpus* and *Avicennia* trees grow up to the top of the ridge, which is from 75 to 125 feet wide along most of its length and averages over 3 feet high.

Besides the shore-fringe mangroves, there are three mangrove communities. A small *Laguncularia* consociates, with *Batis* as an under growth, covers nearly an acre inland from the eastern patch of open-strand plants. A large *Avicennia* associates extends from the sand ridge northward over a wide, shallowly flooded flat area, and a large *Rhizophora* consociates in the deepest-water parts covers about half the island. Boy Key is altogether a mangrove colony, mostly of *Rhizophora* with some *Avicennia* trees in the center.

Barracuda Key

Topography. This is the second largest island of the group near Key West, and covers over 230 acres (fig. 6). A large, shallow pond, of an average depth of 3 feet, covers over a third of the area. Low ridges of sand with some marl extend in a broken chain around the west, north, and east sides. Between these narrow ridges and the pond, and over all the southern part, the island is flooded. Some of this surface water is affected by the tide, but some of it is ponded back of the ridges. No effect of tide on the large pond was observed.

Only a few sand-marl ridges form beaches on the eastern side. The sand ridges of the west side, noted by Millspaugh as fronting on the sea with beaches, are now all shut off from open water by mangroves. The western ridges are about 3 feet high, but the northern and eastern ridges are seldom above a foot. These latter must be of recent origin and seem to be building up rapidly. The long southern tongue of the island seems to have shortened, and some of the open-water areas of the southern part have filled up with mangroves. How Lansing failed to note the large interior pond is a question, as it has been known by fisherfolk for as long as any have visited the island. Lansing evidently did not penetrate the interior of this or many of the other mangrove-clad islands.

Vegetation. All the key except the sand-marl ridges is a mangrove swamp of two fairly distinct communities. Over the shallow-water flats around most of the pond is a thicket growth of *Avicennia* with little or no salt-marsh herbage. This is a typical scrub *Avicennia* consociates. *Rhizophora* forms a scrub consociates on similar flats to the east and south of the pond. Larger red, black, and a few white mangroves grow over many parts flooded

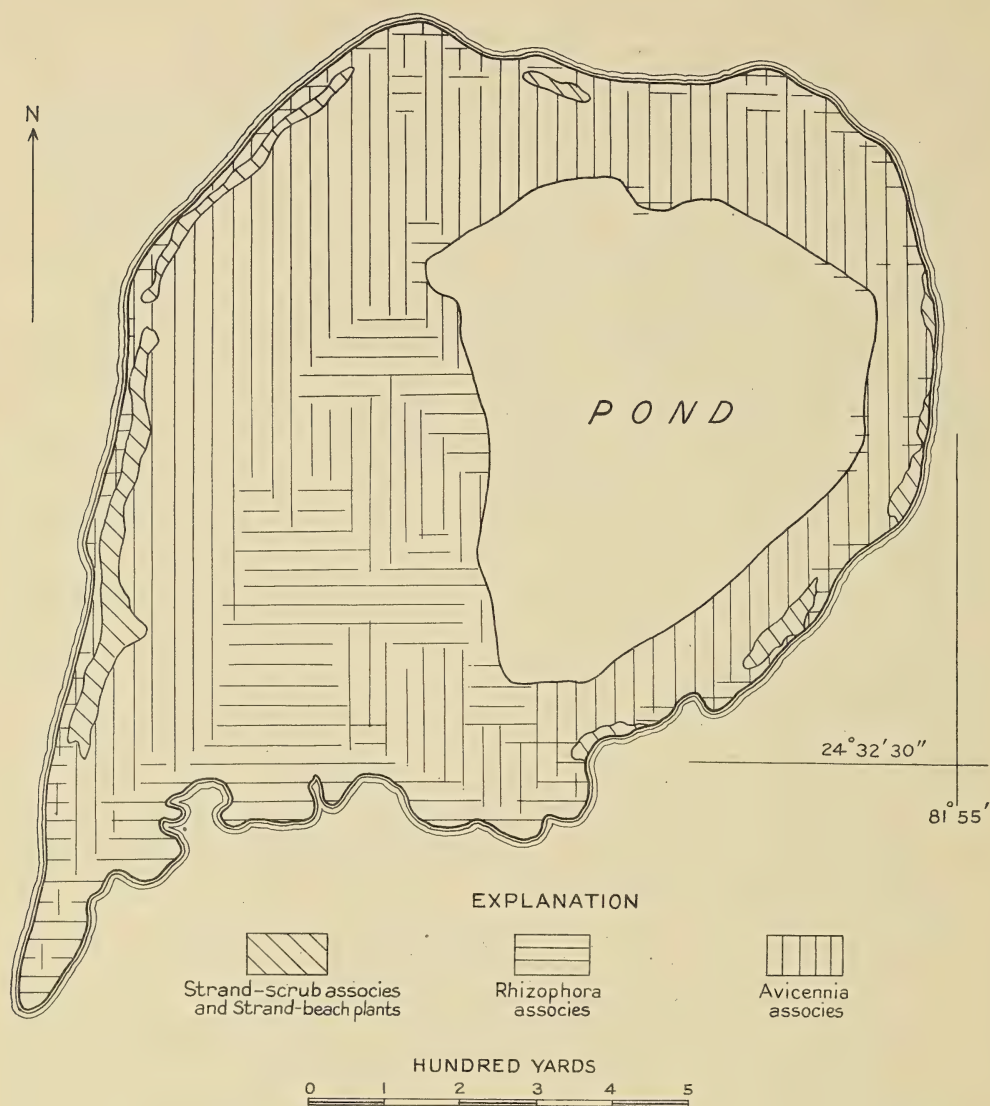


Fig. 6. Barracuda Key

by deeper water than the scrub flats. *Rhizophora* and *Laguncularia* are most frequent along the shore.

The highest sand ridge parallel to the western shore is an old strand-dune associates that in some places is almost a scrub or hammock associates. *Conocarpus* and *Pithecolobium guadalupense* are the largest trees, with a number of old *Avicennia* trees over parts of the ridge bordering the mangrove swamp. Over most of the ridge there is a sparse growth of strand-dune plants: *Melanthera*, *Cyperus*, *Andropogon*, *Hymenocallis*, *Dondia*, *Opun-*

tia, *Calonyction*, *Sporobolus*, and a few *Suriana* bushes. The absence, or small number, of *Lantana*, *Solanum*, and *Gullandia* is difficult to explain in a situation where conditions are so similar to those in many of the strand-scrub associates of which these plants are fairly constant members (table 2).

The low sand and marl ridges that border on the northern and eastern shores form a few short beaches where fringing mangroves have not grown out in the shallow water in front of them. On these beaches and ridges are mixtures of the salt-marsh and strand-beach plants, forming colonies without any definite associates character. The most frequent plants are *Batis*, *Sesuvium*, *Borrchia*, *Panicum amarulum*, and *Dondia*. Where the mangroves grow large, they may shade the entire ridge. The higher and the sandiest of these ridges have *Suriana* and other shrubs typical of the strand scrub.

Other mangrove-covered islands were not studied in detail, but their vegetation is much the same as that of Barracuda Key except that none of them has so extensive a sand ridge with strand vegetation. In general on these islands *Rhizophora* and *Laëuncularia* grow in the deeper-water parts, surrounding *Avicennia* in the shallow-water parts of the interior.

THE MARQUESAS ATOLL

Topography

Some of the main features of the elliptic Marquesas atoll and the probable mode of its formation have been pointed out above. The islands now present around the shallow channels and shoal water of the interior basin are located and given identification numbers in figure 7. Although there are about twelve islands and islets and a number of isolated small mangrove colonies, these can be considered in six main groups. From the southwestern end of the atoll proceeding around the ellipse clockwise they are: I, Southwest Key, now two islands but recently three and in 1904 only one; II, the Rookery Keys, a group of two small sand islands and a large mangrove colony; III, Long Beach Key, in three parts: two sand-strand areas, one at each end of the crescent, and a long, low connecting area of mangrove swamps; IV, a large island, with only a small sand-strand area at its southern end, that has no accepted name, for convenience here called Southeast Key; V, two small islands that seem to have been formerly one, now known by fishermen as the Gull Keys; VI, a small circular island named Round Island on old U. S. Coast and Geodetic Survey chart 170; and VII, Mooney Harbor Key, by some termed Conch Key.

All the islands, with the probable exception of one (Millspaugh's B), are now present that were described by Millspaugh, but many of these have changed in size and shape and have divided since that date, 1904. Southwest Key has been divided into three parts and is now in two; the two Gull Keys were formerly one island; the Rookery Keys have changed in size. In general there has not been as much growth or coalescence of islands as might have

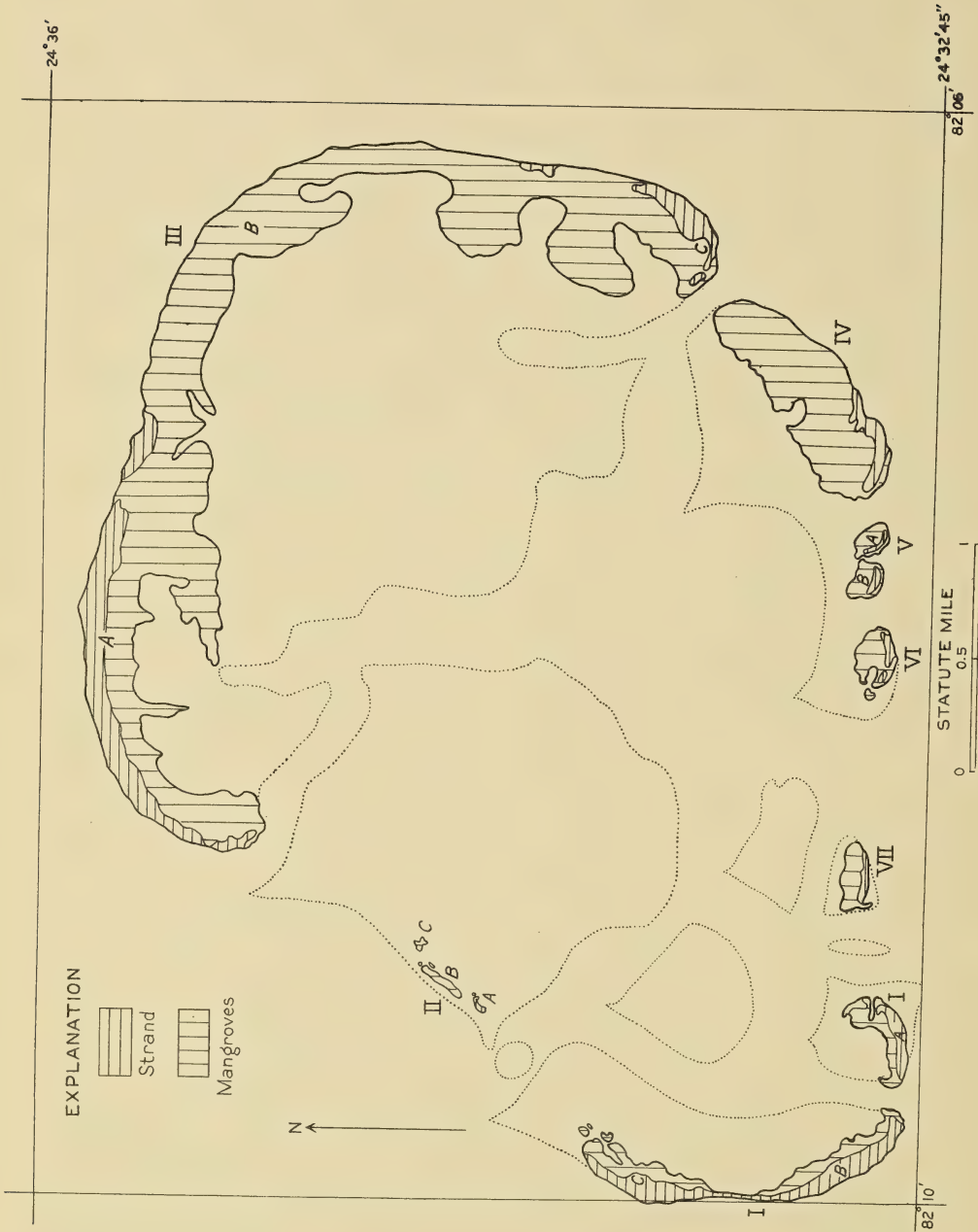


Fig. 7. Marquesas Keys. I, Southwest Key; II, Rookery Keys; III, Long Beach Key; IV, Southeast Key; V, Gull Keys; VI, Round Island; VII, Mooney Harbor Key.

been expected. Millspaugh, after describing some of the factors of accretion, says, "All of these natural forces are uniting to form, in course of time, a solid island embracing this whole group." Such a tendency to form an unbroken ellipse is not present, for the tide and other currents must force their way into and out of the central basin. The southeastern channel, between the southern end of Long Beach Key and Southeast Key, has widened instead of decreasing. The southwest channel has split into at least two parts, one of which now flows through the cut made by a hurricane between parts A and B of Southwest Key.

The shoal areas seem to be extending and the deeper-water parts narrowing. The data on soundings indicate a gradual filling in of the center of the atoll and extension of shoals outside the fringe of islands, especially southward. The total land areas of all the islands have not increased greatly, except that if Millspaugh's measurements of the smaller islands are anywhere near correct, the Gull Keys, Round Island, and Mooney Harbor Key have increased many times. For instance, he gave the sand strip on Mooney Harbor Key as 100 by 25 feet, whereas the island now has a southern sand plateau over 1500 feet long and 150 feet wide. One of the two Gull Keys was then a small islet of about 15,000 square feet, whereas the sand areas of the two are now over 130,000 square feet. The sand areas of the larger islands have not increased as greatly. The swamp areas of all of them seem to have increased.

Comparison of old and recent surveys shows that the ring of islands is closing up to some extent on the southern side by reason of the enlargement of the individual islands, and probably the mangrove swamps are extending farther into the central shoal areas back of all the islands. It is probable, however, that the Marquesas Keys will remain a broken ring of islands for many years to come, because storms will continue to cut passages between them and the channels will keep their openings into the basin of the atoll.

Details of each island will bring out further topographic features and changes. They will be taken up in order from Southwest Key clockwise around the ellipse.

Southwest Key

Topography. The present island is in two parts, and has recently been in three, A, B, and C of figure 8. Probably since 1910, B and C were cut off from A by a storm, and they are now separated from it by a 550-foot channel with a strong tidal current which will probably keep them from growing back to the main part of the island. Millspaugh's description of the island for 1904 shows it all in one piece and about $1\frac{1}{2}$ miles long. The total length of the three parts is now 3000 yards, and therefore has increased, particularly if the eroded gap between parts A and B is included. The width

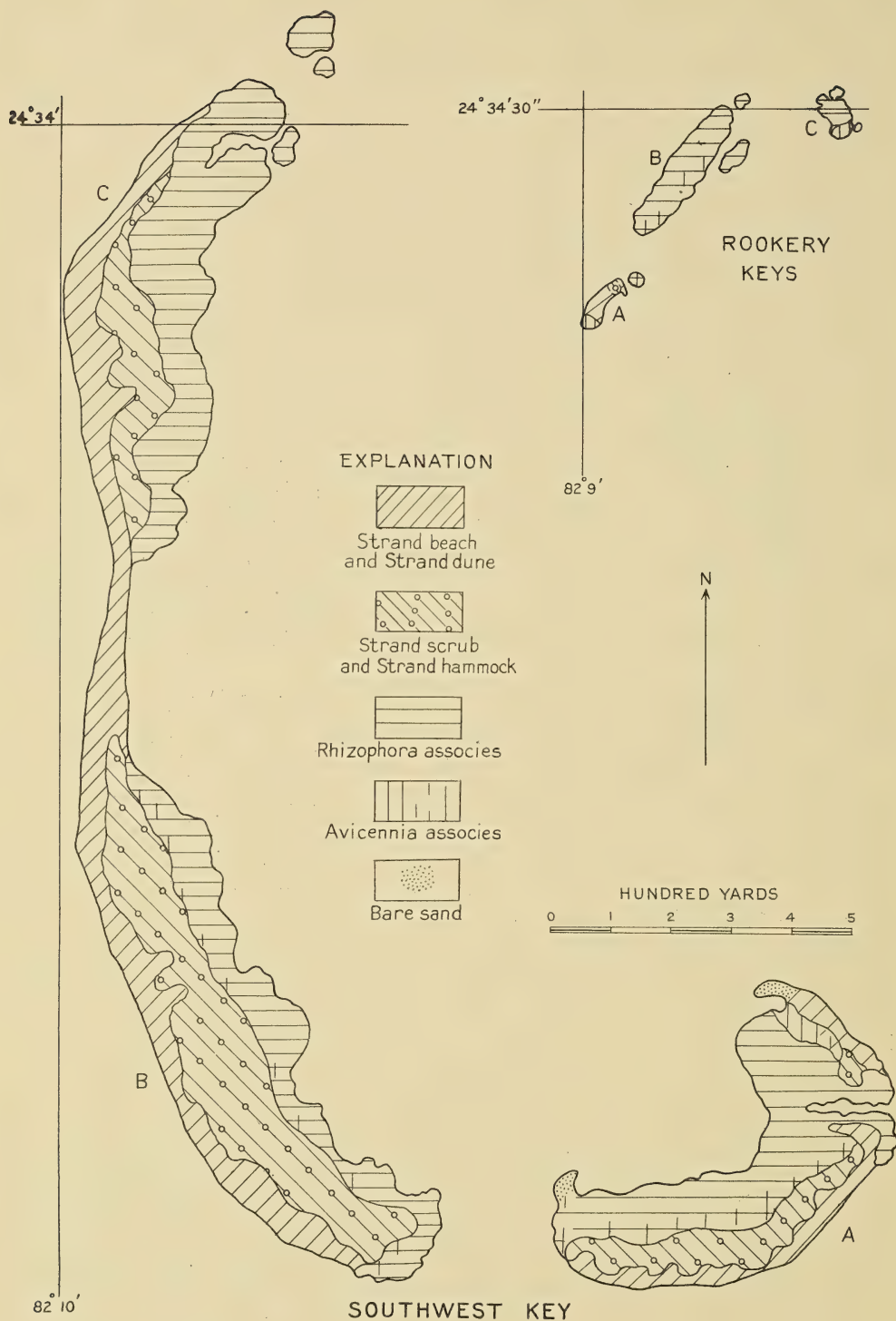


Fig. 8. Southwest Key and Rookery Keys

of the sand plateau now averages over 400 feet, whereas Millsbaugh noted it as 300 feet wide. Thus the total area of the present parts is materially larger than in 1904, although the island has been divided twice by hurricanes since that date.

The gap that has filled in between parts B and C was shown as water in U. S. Coast and Geodetic Survey chart 1252, from surveys to 1921; but probably the surveys were earlier for this Marquesas group, so that it is probable that the gap has been filled within the past 25 years. The sand area is now from 75 to 200 feet wide and averages about 2 feet in elevation.

The northern part of the island has a narrower sand plateau than the southern part. The eastern part has two sand hooks projecting back toward the shallows of the interior of the atoll, and they are probably beginning to round out the shape of this part to make it similar to that of other islands of the southern border of the atoll. The dune plateau has from 3 to 5 feet elevation, and its width and well developed vegetation indicate that the sands have been well stabilized.

Vegetation. Only a narrow beach skirts all three parts, so that there are few of the strand-beach plants except on the new soil that has filled in the gap between the northern and southern parts. Here the pioneer plants are mainly *Sesuvium*, *Dondia*, *Tournefortia*, *Uniola*, and *Suriana*, indicating that these plants are important in the stabilization of recently formed land.

The strand-dune associates covers a belt about 100 to 200 feet wide, with *Uniola*, *Andropogon*, *Chamaesyce*, *Canavali*, *Sporobolus*, *Tymenocallis*, *Ambrosia*, *Flavaria*, and *Tournefortia* the most frequent plants. *Suriana* and a number of bushes of the more interior strand scrub occur as individuals or in patches.

The shrub zone is a transition type of strand-scrub associates which in some places is almost well enough developed to be considered a young hammock. *Pithecolobium*, *Metopium*, *Coccothrinax jucunda*, and *Conocarpus* are the important plants of this most highly developed vegetation. *Lantana*, *Suriana*, *Ernodea*, *Borrchia*, *Melanthera*, and *Ambrosia* are plants of the more typical scrub associates.

Mangrove swamps flank the strand vegetation on all three parts of the island. The swamps are relatively narrow, and there is no distinct zonation of *Avicennia* and *Rhizophora*; these two, with *Laguncularia* less frequent, form a mature mangrove associates.

Rookery Keys

Topography and vegetation. The group of three small islets and mangrove colonies about a thousand yards northeast of the northern end of Southwest Key are here collectively termed the Rookery Keys because the largest of the three is now a mangrove colony where a number of pelicans and herons

roost and nest. Millspaugh describes three small islets of this same locality, identifying them as Marquesas B, C, and D, but he does not indicate their distance from one another or from neighboring islands. The forms and sizes of the group have changed so much since his description that it is impossible to be sure of the identity of the present islands. His B has probably disappeared or is now only the mangrove colony about a hundred yards north of the northern tip of Southwest Key. His C is probably the same as the present A of the Rookery Keys as shown in figure 8, and his D is probably the same as C in the same figure. The present mangrove swamp B, in the same figure, is probably a recent growth of mangroves in the shoal waters, as there is no exposed sand here and the trees all seem to be young enough to have grown since 1904.

If the above correlations are correct, then Millspaugh's C, which was 250 by 50 feet with a central plateau 3 feet above tide, is now 279 feet long and between 40 and 90 feet wide, with only a low strand that is frequently awash in time of storm. The few remains of a strand-scrub vegetation and a colony of mangroves, together with the evidences of wave erosion, indicate that the island is being destroyed. It probably grew somewhat after Lansing's survey and is now decreasing in size. The present vegetation consists of one small patch of *Pithecolobium* at the north end, and a few *Suriana* bushes and *Chamaesyce*, *Dondia*, *Sesuvium*, and *Sporobolus* scattered over the low sand. A few of all three species of mangroves occur at the southern end and as a small colony in the water offshore from the northern end.

The present island B of the Rookery Keys is a 600- by 200-foot colony of vigorous mature mangroves forming a thick growth in shoal water about 18 inches deep. *Rhizophora* is most abundant, frequency about 90 per cent, but both *Avicennia* and *Laguncularia* are present. As is the case with many such mature mangrove colonies used as rookeries, the probable development of this island is uncertain. Many of the trees may be killed by the birds. The shoal may build up to higher levels and a non-inundated island be formed. So far, little peat or muck has accumulated with the marl-mud soil of the mangrove colony.

The third island is about 400 yards northeast of island A, and may be the same as Millspaugh's Marquesas D. It is now only a small, low sand beach about 90 by 25 feet, surrounded by a growth of *Rhizophora* and a few *Avicennia*. *Dondia* and *Sesuvium* are the main plants on the sand area.

Thus we see that the Rookery group is little more than the probable remnants of two former small low sand islands, together with a new mangrove colony. Millspaugh supposed that his group would consolidate into a future larger island. The failure of the group to grow is probably due to the destructive action of storms and the changes in currents affecting the accumulation of sand in this section of the atoll.

Long Beach Key

Topography. Long Beach Key is the longest and largest of all the islands of the Sand Keys. It extends in a great crescent, the total length of its outer shore line being about 5 miles. Both ends of the crescent have sand beaches and dune plateaus, but most of the central part is of such low relief that mangroves cover nearly all of it (fig. 9). This indicates that the southeastern and northwestern horns of the island were probably built up first, or at least have been more rapidly built up, and that the mangrove swamps are a bond between these two parts, perhaps adding land that may eventually form a connection composed of soil above high tide.

The currents that caused the building up of this island have been discussed above. The sediments and detrital material were swept most abundantly toward its two horns, with selective sorting of the finer from the coarser materials, the latter being carried along and deposited at the two ends to form the beaches and dunes, and the sediment of finer materials accumulating on shoals between the horns to form the central mangrove swamp.

The northwestern beach-dune plateau extends from the northwestern end of the island northward then eastward for about 2 miles, and this long beach gives the island its name. The beach-dune plateau at the southern end extends only 650 yards northward along that horn, but there are a number of short, broken beaches northward from it, so that the mangrove connection is not continuous. Since Millspaugh failed to note one of these eastern beach areas about 280 yards in length, it is entirely possible that beaches are increasing along the outer border of the island. The strong flow of currents through the southeastern channel at the southern end and through the northwestern channel at the western end of the island may retard or even prohibit any extension of the island in the direction of its two horns.

The inner shore is very irregular and is entirely covered by mangrove swamps over the low areas that face the inner lagoons. These low swamp areas average about 300 yards in width back of the strand plateau and extend across the island at its low middle part. The dune plateau averages about 200 yards in width and has a maximum elevation of about 6 feet. This sand strand is about 250 acres in area, or much larger than the strand part of any other island studied. The beaches are very narrow, and a steep wave-cut terrace about 3 to 4 feet high usually rises to the dune plateau. Along most of the northern shore the dune plateau is relatively wide and has been so well stabilized that it has developed the most mature strand-hammock vegetation of any of the islands of the Sand Keys.

Vegetation. Distinct zonation of the plant communities is apparent on this island, and all the strand and mangrove communities are well developed. The extensive western and northern strand has a better-developed vegetation than the southern strand area.

The strand-beach associates is almost absent, because of the narrowness of

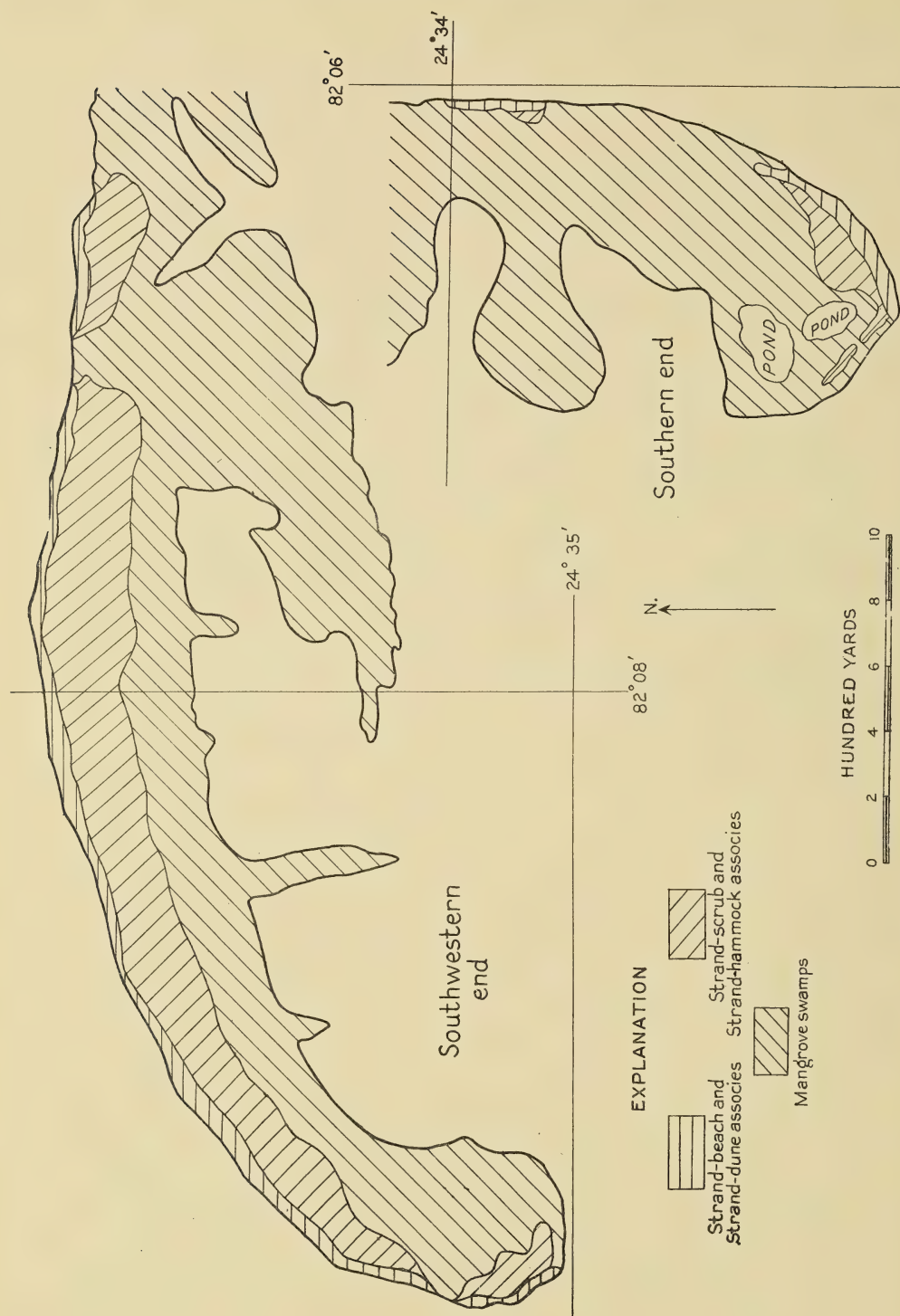


Fig. 9. Long Beach Key: two strand parts

the beach and the abruptness of the dune terrace. Irregular patches of *Sesuvium* and other upper-beach pioneer plants are most frequent toward the extreme western and southern ends of the island.

On the face of some of the dune terrace and extending about 50 to 75 yards inland over the dune plateau there is a long, almost continuous strand-dune associates. The dominant plant is *Uniola paniculata*, with some others of the common grasses, such as *Andropogon* and *Spartina*, locally abundant. *Waltheria*, *Flavaria*, *Chamaesyce*, and *Ambrosia* are some of the most frequent associates. The almost complete absence of *Tournefortia* is difficult to explain. Over this outer zone of the dune plateau occur many of the shrubs and trees of the strand hammocks. *Coccothrinax jucunda* is a common native palm; *Cocos nucifera* and *Phoenix* palms have been planted. The latter were planted in 1910 by Mr. Saunders, one of the guides who accompanied me on the trip in 1940.

Millspaugh noted that a charcoal burner's cabin was once located near the east end of the northern part of this strand area, and Mr. Saunders told of having lived on the island at intervals about 30 years ago. These habitations probably account for the presence of some of the plants found there now or formerly, for example a few royal palms (now dead), *Agave americana*, *Coccolobis uvifera*, and the date palms. Mr. Saunders raised a few tomatoes and other plants, and no doubt all the settlers and their stock destroyed or altered some of the vegetation; but few effects of this activity can be noted now. An interesting fact is that they could obtain a certain amount of nearly salt-free water by seepage into deep holes they dug in the dune plateau. This shows that much of the salt is leached out of the sands by the rains.

Back of the outer *Uniola* strand-dune associates, a thick growth of many different trees, shrubs, and vines forms wide strand-hammock associates. The hammock zone extends on across the island until it meets the inner margins of the mangrove swamps. Over much of the dune plateau this hammock zone is over 200 yards wide, and the vegetation is as nearly climax as any encountered in the investigation. The most frequent and constant species of this associates are *Pithecolobium guadalupense*, *Coccothrinax jucunda*, *Metopium toxiferum*, *Reynosa septentrionalis*, *Gymnanthes lucida*, *Erithalis fruticosa*, *Capparis jamaicensis*, *Panicum divaricatum*, and *Eugenia buxifolia*. Many other trees, shrubs, vines, and epiphytes are to be found. The growth of the low trees and shrubs is thick, and there is little or no herbage on the forest floor. This is by far the best-developed strand-hammock forest of any on these islands.

Between the thick growth of the mature hammock forest and the open, dominantly grassy plain of the strand-dune associates there is usually a scattered growth of transitional shrubs forming a strand-scrub associates. *Suriana*, *Lantana*, *Solanum*, *Coccothrinax*, *Ernodea*, *Smilax auriculata*, and

Pithecolobium guadalupense are some of the most frequent species. Both *Lantana* and *Solanum* are less abundant here than in similar associates on other islands of this group.

In contrast with the western and northern strand area, the southeastern strand area has a poorly developed strand-hammock associates of only a few of the typical species. Most of the area inland from the strand-dune associates has developed no farther than the strand-scrub associates stage. The strand-dune associates is about 80 per cent *Uniola* with other typical species. Some species of the strand-beach associates occur on the upper beach areas and over low parts of the dune plateau. The lack of a well developed strand-hammock associates seems to indicate that this end of the island is younger than the northeastern end, a conclusion contrary to that reached by Mills-paugh.

On the broken beaches northward from this southeastern strand area are found some of the typical plants of strand vegetation. The longest of these beaches is 280 yards long and is 600 yards north of the strand area. It is of low relief, with the strand-beach species abundant. A small area of strand scrub is developing near its southern end and near the interior mangrove swamps.

Southeast Key

Topography. Southeast Key (fig. 10) is the largest of the chain of five islands along the southern border of the atoll. The deep southeast channel separates it from the southern horn of Long Beach Key and probably will keep the two islands from ever growing together. The entrance to this channel is known as Southeast Harbor, and the island is sometimes called Southeast Harbor Key by fishermen.

This island is over 4200 feet long and averages 1200 feet wide, but only a small part of the southwestern end is strand. Millspaugh noted a sand ridge with a beach continuing around the southeastern tip of the island, but since then mangroves have grown around this tip and the beach line is much shorter. This tendency for mangroves to grow in the offshore shallows is common to all the southern keys of the atoll. Such a growth probably indicates that sediments have recently become more abundant in the shoal waters, and the coarser materials that form the beach less abundant. Also the waters are probably quieter. Both these interrelated factors aid in the spread of mangroves along shores that were formerly bare sand beaches.

The sand plateau and beach are now over 2100 feet long and about 90 to 250 feet wide, with an average elevation of 3 feet. The remainder of the island consists of flooded or low-elevation mangrove swamps. A few low beaches occur along the eastern shore north of the sand plateau. A large pond lies 150 feet inland from the sand ridge.

Vegetation. The greater part of the strand area is given over to a

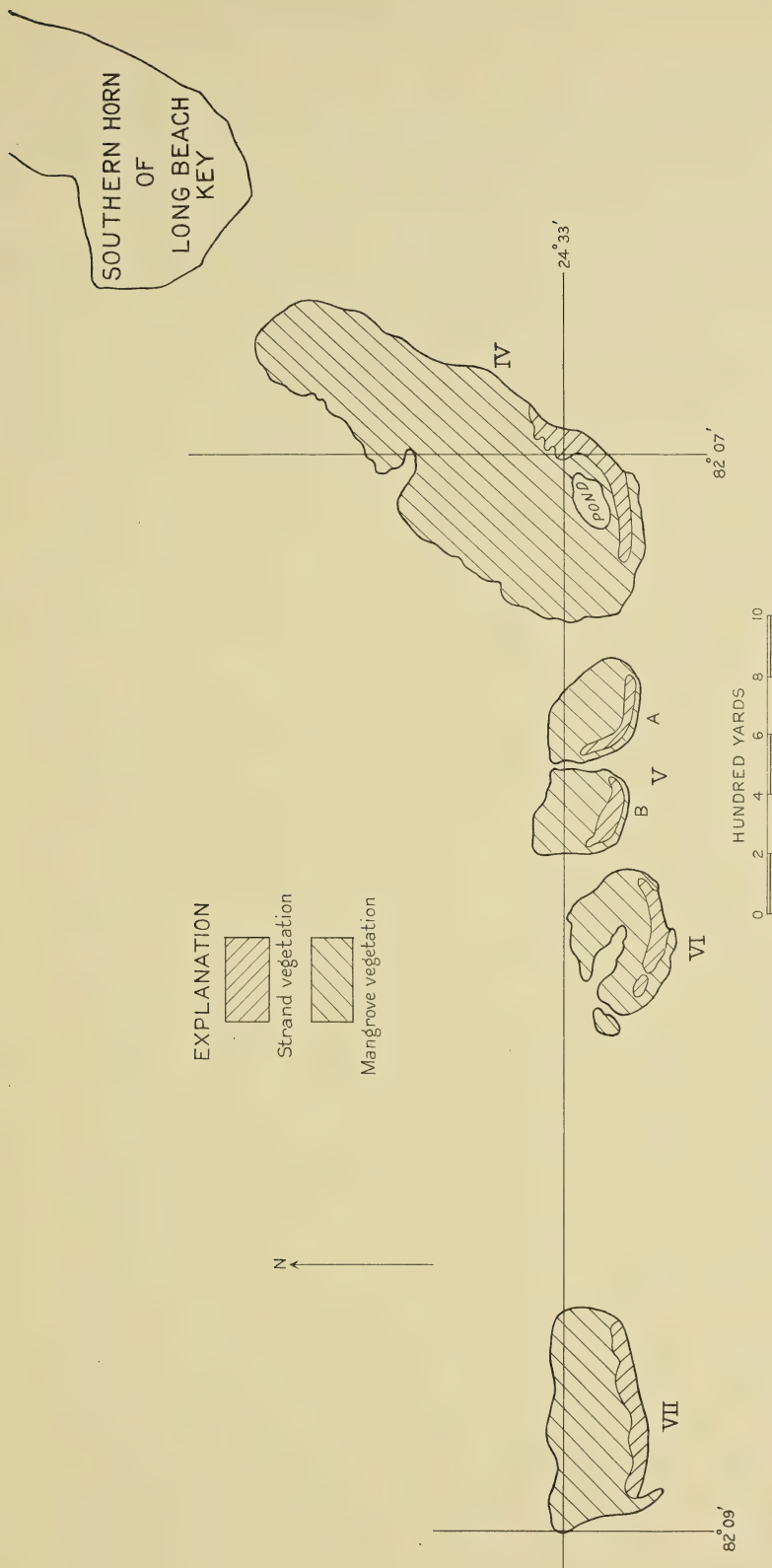


Fig. 10. Southern Islands of Marquesas Keys. IV, Southeast Key; V, Gull Keys; VI, Round Island; VII, Mooney Harbor Key.

Uniola-dominated strand-dune associates, but there are well developed areas of strand-scrub plants associated with the trees, *Conocarpus* and *Avicennia*, that grow near the inner borders of the plateau. *Suriana*, *Ernodea*, *Solanum*, *Chloris*, *Hymenocallis*, *Borrchia*, *Iva*, *Lantana*, and *Melanthera* are the most frequent of these plants.

Over the strand-dune areas *Uniola*, *Waltheria*, *Ambrosia*, *Andropogon*, and *Canavali* are the typical plants. *Suriana* and *Tournefortia* occur frequently. In one low swale there is a group of black and white mangroves.

There are large areas of black mangrove flats around the pond and flanking nearly all the strand plateau. A few Australian pines, *Casuarina*, have begun growth on the low shore ridges just north of the strand plateau. Most of the interior and inner shore areas are a *Rhizophora* associates swamp.

Gull Keys

Topography. The development of these two small islands is something of an enigma. Millspaugh locates only one at this position (Millspaugh's Marquesas G) and describes it as only 200 by 75 feet in extent. Which one of the present two islands this was is uncertain. Both the present ones are of about the same size, their sand areas 3 acres and their total areas over 14 acres. This large increase in size is due to the building up of the strand areas and extension of the mangrove swamps. The two islands are nearly tied together by mangroves, which almost close the narrow passage between them. It is possible that these were one island that split apart, but the direction of development of the strand areas makes this seem unlikely. On the eastern island the strand ridge curves toward the northwest, indicating an independent development (fig. 10).

Both sand areas are without beaches, mangroves fringing the shore, and the sand forming a long, narrow ridge over 3 feet high. Gradual extension of mangroves in shallow water along the beaches is taking place on these southern and some other islands of the Marquesas group, as noted above. The present areas of sand soil will probably not increase in size, because the shore mangroves will inhibit further washing in of coarse calcareous materials. If these islands continue growth it will be mainly through sedimentation in the mangrove areas. Past rapid growth seems to have been due to rapid accumulation of beach and dune sands.

Vegetation. The fringing mangroves are of all three species, with *Avicennia* and *Laguncularia* most frequent in that order. On the sand ridges the strand-dune associates is dominated by *Uniola*, with *Lantana*, *Borrchia*, *Melanthera*, *Panicum amarulum*, and *Cyperus* the most frequent associates. No strand-scrub associates has developed. *Batis* is common among the shore mangroves, and *Dondia* and *Sesuvium* on the low, open sand areas. In the interior there are large areas of *Avicennia* with *Batis*, but *Rhizophora* forms most of the swamp.

Round Island

Topography. Millspaugh wrote, "This small key is 1200 feet in area," but now it is about 1200 feet in diameter. If he meant 1200 square feet, then the size of the island has increased 1200 times, which seems very improbable. He must have meant that the length was 1200 feet. Round Island has probably increased as much in size as the neighboring Gull Keys, for Millspaugh described the strand as so new and small that the plateau was barren of vegetation.

The present strand plateau averages 3 feet in elevation and is about 900 feet long, with a beach strip 350 feet long. The fringing mangroves are growing out in front of the strand. A large embayment enters the low mangrove areas of the northwest side, and a large mangrove colony has developed to the west of the island.

Vegetation. On the strand beach *Sesuvium* and *Dondia* are most frequent. On the strand plateau is a typical strand-dune associates dominated by *Uniola*. The *Rhizophora* associates covers most of the swamp areas.

Mooney Harbor Key

Topography. This island has been known as Conch Key, then Couch Key, and now Mooney Harbor Key. Millspaugh and U. S. Coast and Geodetic Survey chart 170 named it Conch Key. A later U. S. Coast and Geodetic Survey chart, no. 1252, spelled it with a *u* instead of an *n*, probably through some error. The recent chart 1252 names it Mooney Harbor Key.

Millspaugh's description gave the sand strip as very small, 100 by 25 feet, as compared with its present size of 1500 feet long and over 150 feet wide. Such a great increase in area of the strand, and probably a similar increase in area of the mangrove swamps, is hard to explain in so short a time, 36 years. The island is in a good position for relatively rapid accretion, lying near channels where currents can shunt detrital materials and sediments onto the shoal areas about it. But, as in the case of Round Island and the Gull Keys, it may be that some mistake in the measurements made by Lansing for Millspaugh accounts for the apparent great increase.

The present island has only about 200 feet of beach and a small sand bar directed southward from its western end. Mangroves fringe the outer part of nearly all the sand plateau. The plateau has an average elevation of 3 feet.

Vegetation. On the short beach there are a very few places where strand-beach communities have developed. The strand-dune associates is, peculiarly, almost entirely absent, there being no large areas of *Uniola* and its associates. Most of the stabilized land is now occupied by a mixed type of strand-scrub associates and a partly developed strand-hammock vegetation. The latter occurs on the inner parts near the mangrove swamps, and is over 50 per cent *Pithecolobium guadalupense*, associated with *Cono-*

carpus and some of the mangroves near the border between the two types of vegetation. *Hymenocallis*, *Solanum*, *Calonyction*, and *Metastelma* are frequent associates.

The strand-scrub areas have some *Uniola*, *Chamaesyce*, *Flavaria*, and other strand-dune plants, but *Lantana*, *Solanum*, *Melanthera*, and *Cyperus*, which are more typical of the strand-scrub associates, dominate most areas. The scarcity of *Suriana* and *Tournefortia* bushes is striking.

THE TORTUGAS KEYS

Topography

At present there are only six islands in the group that form the Dry Tortugas Keys, but formerly there were eight (see fig. 1). The largest of these is Loggerhead Key, resting on the central part of the elongated southwestern bank of the atoll. At present Loggerhead Key is about 4500 feet long and averages about 600 feet wide. It has been extended about 350 feet toward the southwest and 200 feet toward the northeast in the past 25 years. Garden Key, the second largest island over a long period of years, is now no larger than Bush Key, across the harbor channel from it. Garden Key has retained its approximate size since the last construction work was done on the buildings of Fort Jefferson, at the beginning of this century. Bush Key has increased greatly in size since Bowman's description (1918) of the island from surveys of 1916. Bird Key, which was 500 feet long and 300 feet broad in 1916, had completely disappeared by 1935 and is now beginning to reappear. Long Key has increased in size and elevation. The three small islands that extend from East Key, on the southern horn of the northeast bank, westward to Sand Key have each seldom if ever been larger than about 2000 feet in circumference. Sand or Hospital Key and East Key have been fairly stable in size and shape, but Middle Key has repeatedly appeared and disappeared. It was last destroyed in 1938, but shows some signs of returning.

Thus we see that the islands of this group have been altered a great deal from time to time; at present they are fewer in number than usual, but some of them are larger than formerly. As pointed out above and by Vaughan (1914), the constructional processes that cause the accumulation of coarse calcareous sand to form these islands on the coral banks are mainly influenced by marine currents. These currents shift about from time to time and may cause the destruction of part or all of an island. The land plants play no part in the primary formation of the islands, but they materially retard erosion, especially by storms and surface currents. The thousands of terns and other birds on Bird Key aided in the destruction of the vegetation, and the loss of vegetation contributed to the destruction of the island. Human activity around Garden and Bush keys, in the building of the fort and the dredging of the harbor and channel, altered the size and shape

EXPLANATION

Suriana consocios

Chamaesyce associates

Uiola strand-dune associates

Sesuvium consocios

Panicum maximum

Salicornia

Opuntia

Iva

Scaevola

Achynanthes

Hymenocallis

Cocos

Date palms

Conocarpus

Other trees and shrubs

Avicennia

Tournefortia

Guilandina

R
Rhizophora
A
Agave americana
P
Scaevola
Pa
Carica papaya
B
Batis
G
Geiger tree
O
Agave sisalana
U
Coccolobis uvifera
Cy
Cyperus
Ce
Cenchrus
L
Laguncularia

CARNEGIE
LABORATORY

LIGHTHOUSE
GROUNDS

82° 52'
24° 37' 45"

FIG. 13

FIG. 11

FIG. 12

0 1 2 3 4
HUNDRED YARDS

Figs. 11-13. The principal islands of the Tortugas Keys. For actual relative positions, see figure 1.
Fig. 11, Loggerhead Key; fig. 12, Garden Key and Fort Jefferson; fig. 13, Bush Key and Long Key.

of those two islands. Detailed records of these changes are difficult to obtain, even though much has been published about the islands and long records of construction and dredging at Fort Jefferson have been kept. For the most part, only major changes definitely occurring within the past 40 years are considered here, and any inaccuracies in the statements regarding these changes can be traced to lack of reliable information.

The interesting history of this often visited group of islands seems to be partly legendary. Gifford (1934, p. 28) says, "These [islands] were named by none other than Ponce de Leon who in June 1513 captured one hundred and seventy turtles on these beaches." Since that early date there have been numerous descriptions of the islands, but few of them are of any scientific value. Some of the history of the group is outlined in the description of Garden Key.

Vegetation

Only three of the islands, Loggerhead, Garden, and Bush keys, are large enough to support the development of distinct plant communities. The plants on East and Sand keys and on newly formed sandy parts of the other islands are scattered individuals of the strand-beach and strand-dune associates, forming at most small colonies. The plants on the low coral-fragment reef that forms Long Key are a few scattered mangroves and families or colonies of three species of beach and salt-marsh plants, *Salicornia*, *Sesuvium*, and *Batis*. Even on the larger islands the plant communities do not occur in the fairly regular zones so characteristic of the communities of the other islands of the Sand Keys. The native vegetation has been greatly altered on Loggerhead and Garden keys by the clearings for buildings and around them, and by the planting and spread of ornamental and fruit plants. Many exotic weeds have been introduced, and some of these have altered the composition of the native flora enough to change the character of the communities. A list of both these types of plants is given in table 7. Fires have also caused some destruction and alteration of the vegetation.

After all non-natural conditions have been eliminated so far as possible, about seven distinct plant communities may be recognized. Bowman recognized four such communities, and Millspaugh failed to recognize any, except possibly a *Suriana* consocieties. Definite large-area communities with a number of species in each are notably lacking. Many of the groups of plants covering small areas are hardly more than colonies or families, of two or one species respectively, that have spread over bare sand areas or crowded out former occupants. The vegetation does not seem to be tending toward any definite climax, being distinctly of a subclimax type. The major communities recognized are: (1) the strand-beach associates, (2) the *Uniola* strand-dune associates, (3) the strand-scrub associates, almost entirely made up of a *Suriana* consocieties, (4) the *Opuntia* associates, (5) the *Chamaesyce* associates, (6) the *Agave* associates, and (7) the *Laguncularia* associates.

The strand-beach associates is a very heterogeneous community, composed of the many pioneer plants of the upper beach and the newly formed or nearly bare sand plateau areas. Most of the plants are in small colonies or families, and locally certain species such as *Sesuvium* cover large enough areas to form consocieties. Nearly all the plants of the other communities may occur in this associates as scattered individuals or in small groups.

The *Uniola* strand-dune associates is distinguished by the dominance of *Uniola paniculata*, and covers some large areas on Loggerhead and Bush keys. The species associated are similar to those of the other islands of the Sand Keys, but a distinction between the *Uniola* strand dune and the areas dominated by *Chamaesyce buxifolia* is made here because this latter plant forms with a number of weed species a fairly distinct community of its own.

The strand-scrub associates is not a mixed community with a number of species, but is dominated almost entirely by the bay cedar, *Suriana maritima* (pl. 3, fig. 1). This shrub forms a close stand, excluding nearly all other plants, and the community is therefore described here as the *Suriana* consocieties. This *Suriana* vegetation is probably the climax type of the Tortugas islands, as the death of *Suriana* usually leads to retrogression; the three following communities develop on the same soil areas, which become drier after the death of the bay cedars.

Opuntia (pl. 4, fig. 3) and a few coarse grasses form a fairly distinct community, but the cacti are usually distributed in the *Suriana* community or the *Chamaesyce* community.

Chamaesyce covers large areas on Loggerhead, Garden, and Bush keys, and seems to grow in situations now unsuitable for either *Suriana* or *Uniola*. With it grow a number of the weeds of these islands, and some of the native plants, *Melanthera*, *Iva*, and others. *Panicum maximum* dominates some areas on Loggerhead Key, with a scattering of *Chamaesyce* and its associates.

Agave americana L., the century plant, has spread to cover some fairly large areas on Loggerhead Key (pl. 4, fig. 2), and in some places forms a fairly distinct community with a number of associated species.

On Bush Key there is now a well developed colony of mangroves, mostly *Laguncularia racemosa*, with a few *Rhizophora mangle*. This thicket forest is around the largest pond on Bush Key, and it is the only mangrove community of the Tortugas.

Besides these seven communities, there are a number of lesser communities, such as an *Achyranthes* consocieties and *Salicornia* and *Batis* families, which will be considered with the individual islands.

Loggerhead Key

Topography. The long axis of the island, now about 4500 feet, seems to have increased 500 feet or more since the survey by Bowman in 1916. The

exact increase toward both ends is difficult to estimate without more accurate data. Bowman's drawing shows a total length the same as or even greater than that of the present island. If his location of the lighthouse is anywhere near accurate, the southwestern end of the island has extended since his survey; but he shows the lighthouse and the Carnegie laboratory much farther apart than they actually are, so that comparison with his drawing is unsatisfactory. The best indications of change are the bare sand areas and the pioneer strand-beach and strand-dune plants that grow on new sand areas. The sand hooks at both ends shift about, and no doubt a loss or increase of a hundred feet at either end may occur within a short period of time. Back of each sand hook there is an abrupt rise of 2 to 4 feet to a dune plateau. These plateaus are relatively stationary, and when plants develop on them they become fairly permanent parts of the island.

The width of the island has not changed much except as it has varied a few feet near the southwest end. The beaches slope steeply and are not wide. On parts of them there is developing a beach rock of indurated calcareous sand that has built up the shore, especially on the west side opposite the lighthouse. Some of this rock underlies part of the deep sands which form the island. No clear account of the processes involved in its formation was found in the literature. Sand Key is the only other island of the Sand Keys on which such rock development was noted.

Probably the most important topographic feature of this island is the height of the central part, which at some points is 9 feet above mean tide. These deep sands are very coarse and well drained, so that they become very dry. This island is the highest of all that were studied.

Hurricanes and storms of the past have undoubtedly changed the shape of the island, particularly at both ends, but accounts of old lighthouse keepers indicate that its general size has changed little. Bowman points out that over 100 years ago the island had a stand of buttonwoods. This would indicate that it was then of much lower elevation, as the buttonwoods probably developed near depressions or ponds as they now do on Bush Key. The island may have begun as a shoal or bar of coral debris on which mangroves gained a foothold, and buttonwoods followed the mangroves.

The few extensions that have taken place at each end within 25 years are becoming fixed by plant growth and may be relatively permanent additions, but again there may be subsequent erosion and changes. Thus Loggerhead Key may be considered as making only slow if any progress toward a permanent increase in size.

Vegetation. Most of this island is covered by a thick growth of the bay cedar, *Suriana maritima*, which forms a *Suriana* consocieties that at present does not seem to be holding its own, but is gradually being replaced by two apparently more xeric plant communities. Between the area of cleared ground and plantings around the U. S. Coast Guard lighthouse and similar

areas around the Carnegie Institution laboratory, there is a large area on both sides of a path that is almost completely covered by this *Suriana* consocieties (pl. 3, fig. 1). Southwestward from the lighthouse buildings toward the tip of the island only about half of the area is covered by this consocieties, for much of the vegetation in this area has been burned or otherwise destroyed and there is much new land. In this southwestern part of the island a large part of the area once occupied by *Suriana* has been taken over by a growth of *Opuntia* (pl. 4, fig. 3); *Chamaesyce*, *Agave americana* (pl. 4, fig. 2), and other plants. In spite of these changes *Suriana* still covers most of the uncleared parts of the island.

Natural causes may have brought about this decrease in *Suriana* areas. Bowman pointed out that *Suriana* "does not withstand a drenching of sea-water very successfully, the tomentum of the leaves holding the water until its toxic effect is produced on the leaf-tissue." Although no storms occurred during the author's visits to the Tortugas Keys and the effects of drenching by salt-water spray were not observed, it does not seem probable that drenching alone accounts for the decrease in these plants. If this were true, *Suriana* would not be so commonly found very near the beach on nearly all the western Florida Keys. It seems more likely that the *Suriana* bushes reach such a size and grow so close together that their roots fail to obtain enough water from the porous soils. Their thick growth forms a dense shade and their roots cover most of the soil, so that few or no plants can live beneath them. *Tournefortia*, *Opuntia*, *Calonyction*, and other plants are sometimes found with *Suriana*, but these associates are not frequent enough to form a community of the grade of an associates.

Next in importance to the *Suriana* consocieties is the *Uniola* strand-dune associates. This plant community covers two fairly large areas southwest of the lighthouse clearing and small areas all along the coast, particularly northeast of the Carnegie laboratory. There is no well developed mixed growth of *Uniola* and other strand plants forming the type of strand-dune associates that is the rule on many of the Marquesas and other islands of this investigation. The community is in some instances practically a pure growth of *Uniola*, forming a consocieties. In general *Uniola* occupies new land areas of the dune plateau. This is particularly true of the areas near the southwestern end of the island.

Between the steeply sloping fore dunes and the beach there are some fairly distinct strand-beach plants, forming a few colonies and families. *Sesuvium*, *Ipomoea*, *Sporobolus*, *Uniola*, *Tournefortia*, and other typical species of areas near the beach are to be found around all sides of the island. These pioneer strand plants are especially abundant over the newly built dune areas near the southwestern tip of the island and over a similar but smaller area near the northeastern tip. *Tournefortia* is very common

along the ridge between the wave line and the upland plateau. *Suriana* is also common along this fore-dune area, and many of the *Suriana* bushes are encroaching on the sand of the upper beach. It does not seem likely, however, that the *Suriana* community develops as often as does the *Uniola* strand-beach associates directly on the first sands that are stabilized above the high-tide level. In general, the pioneer strand-beach associates and the *Uniola* community both precede the *Suriana* consocieties. On the other hand, the *Uniola* consocieties does not seem to be a necessary antecedent to the *Suriana* consocieties in all instances. The first plants on the bare sand areas at the northeastern and southwestern ends of the island include many *Suriana* bushes as well as *Uniola*, *Chamaesyce*, *Ipomoea*, and *Sporobolus*. Moreover, these more definitely pioneer plants in some instances form distinct plant communities farther inland, so that no rigid rule of development can be postulated. Whether or not any one of them occupies the area and obtains control of it seems to depend on competition. Colonies, families, and clans of nearly any species develop freely almost anywhere. Therefore the establishment of a particular plant community on recently formed or older sand areas is not distinctly related to the seral development as found on islands farther east.

A fourth recognizable community is dominated by *Chamaesyce buxifolia*, but other species are nearly as frequent in it. The plants sparsely cover many of the almost bare areas left after the death or destruction of the *Suriana* bushes. These *Chamaesyce* communities usually occur as small inclusions within the broader expanse of the *Suriana* consocieties. Between the lighthouse and the Carnegie laboratory there are a few small areas covered by this associates. Between the lighthouse and the southwestern end of the island there are two fairly large interior areas given over to a mixed growth of *Chamaesyce* and associated species. Many weed plants, such as *Leptilon*, *Boerhaavia*, *Bidens*, *Valerianoides*, and *Portulaca*, invade these areas and are often more abundant than *Chamaesyce*. In some places the areas have been cleared of other plants to let the *Hymenocallis* grow. Many patches of *Opuntia* and small areas dominated by grasses are frequent in or near the *Chamaesyce* associates. Vines, *Calonyction*, and *Canavali* are common. This is the most mixed of all the communities of the island.

A scattered growth of the strand prickly-pear cactus, *Opuntia*, occurs over many areas and forms patches that may be termed an *Opuntia* associates. This community was recognized and described by Bowman. It is made up mainly of *Opuntia Dillenii*, but certain associated coarse grasses, vines, and plants that are also frequent in the *Chamaesyce* associates are locally abundant. This cactus seems to be occupying many areas formerly covered by *Suriana* bushes, and seems to replace the latter in fairly large patches, as the soil becomes drier. In general, however, *Opuntia* is scattered over

many areas occupied by either *Suriana*, *Chamaesyce*, or even *Uniola*. Consequently, it is difficult to show (fig. 11) many areas that are distinctly *Opuntia* associates.

The cleared and planted areas around both the lighthouse and the Carnegie laboratory have been enriched by the transportation of richer soil to the island, by fertilization of the plants, and by other means. The palms, Australian pines, geiger trees, papayas, and other cultivated plants (table 7) on and about these areas are probably growing much better than they nor-

Table 7. *Introduced trees, shrubs, and weeds, Tortugas Keys*

Fruits and ornamentals	Weeds
Agave americana L. (century plant)	Amaranthus sp.
Agave sisalana Perrine (sisal hemp)	Argemone leiocarpa Greene
Aloe vera L. (bitter aloe)	Asparagus sprengeri Regel
Carica papaya L. (papaya)	Atriplex cristata A. & B.
Casuarina equisetifolia Forst. (Australian pine)	Bidens leucantha L.
Cerbera thevetia L. (trumpet flower)	Boerhaavia coccinea Mill.
Coccolobis uvifera (L.) Jacq. (sea grape)	Cajon cajan (L.) Millsp.
Cocos nucifera L. (coconut palm)	Capraria biflora L.
Cordia sebestena L. (geiger tree)	Dolicholus minimus (L.) Medic.
Elaphrium Simaruba (L.) Rose (gumbo limbo)	Heliotropium curassavicum L.
Ficus carica L. (common fig)	Leptilon canadense (L.) Britt.
Ficus hispida L. (African fig)	Lithophila vermicularis Uline
Hibiscus rosa-sinensis L. (Chinese rose)	Phyla nodiflora (L.) Grave
Nerium oleander L. (oleander)	Portulaca oleracea L.
Phoenix canariensis Chaub. (date palm)	Salvia serotina L.
Phoenix dactylifera L. (date palm)	Sesbania macrocarpa Wuhl.
Psidium guajava Raddi (guava)	Sida sp.
Ricinus communis L. (castor-oil plant)	Sonchus oleraceus L.
Tamarindus indica L. (tamarind)	Tithymalus Smallii (Millsp.) Small
Terminalia catappa L. (Indian almond)	Valerianoides jamaicensis (L.) Kuntze
Thespesia populnea (L.) Soland (portia tree)	
Vinca rosea L. (periwinkle)	
Yucca aloifolia L. (Spanish dagger)	

mally would had they been introduced through natural agencies and left to grow without encouragement. *Casuarina equisetifolia*, the Australian pine, has spread by natural means outward from the original plantings, and seedlings are growing over many parts of the island. It seems entirely probable that these trees will continue to grow whether or not they are cared for, and eventually they may replace some of the present vegetation, for after they have become large few plants can live under them. Some of them are now spreading southward from the cleared area around the lighthouse and are definitely taking over areas formerly occupied by other plants in that part of the island. Another cultivated plant that seems to be at home on the island is the coconut palm, *Cocos nucifera*. It grows well and fruits abundantly where it has been planted, but so far does not seem to spread by

natural means. Both the century plant, *Agave americana*, and the true sisal hemp, *Agave sisalana*, were probably planted on the island, but have spread. Most of the other cultivated plants, such as the oleanders, *Hibiscus*, *Thespesia populnea*, *Aloe*, *Yucca*, and figs, have not spread far from their original locations, if at all. These plants, with the exception of *Agave*, are not shown in any detail on the map of the island, figure 11, because they are not a definite part of the natural vegetation. A row of coconut palms along the path southward from the Carnegie laboratory is shown, but these are only a few of the many to be found planted around the dwellings of the laboratory and of the lighthouse.

Although more trees and shrubs have been planted on this island than on Garden Key, there are fewer of the maritime weeds here. No doubt many of these weeds have been brought to the islands by visitors and inhabitants over a long period of years, but none of them seem to have replaced any appreciable amount of the native vegetation. A few of the commonest of the weed species on Loggerhead Key are *Leptilon canadense*, *Boerhaavia viscosa*, and *Bidens leucantha*, which grow abundantly either in the *Chamaesyce* associates or around the dwellings. There seems to be little indication that any of the introduced plants except the Australian pine and perhaps *Agave* will become sufficiently abundant to alter the native vegetation.

Clearing and encouragement by man have increased the number of the beautiful spider lilies, *Hymenocallis keyensis* (pl. 3, fig. 3). These plants cover a fairly large area northward along the path between the lighthouse and the Carnegie laboratory. They grow naturally in the openings of the *Suriana* consociates and in some parts of the *Chamaesyce* associates.

Large patches of *Agave americana* (given as *A. rigida* by Bowman) cover areas south of the lighthouse and three small areas north of it. These patches seem to be increasing in size, and the plants seem to be spreading over many of the areas formerly occupied by *Chamaesyce*. These plants may be considered as forming an *Agave* associates similar in many ways to the *Opuntia* associates. This and other species of *Agave* are to be found with the strand vegetation of many of the islands of the Florida Keys, and it should not be regarded as having been established only by human agencies.

To summarize: As Loggerhead Key has developed extensions northeast and southwest, the bare sand areas have been rapidly taken over by the strand-beach and strand-dune plants. The sands are blown or washed up to higher levels above the beach than on any other island studied, and high, fairly level plateaus are formed. The largest such plateau now developing is at the southwest end, and the greatest extension of the island since Mills-paugh's time has been in this direction (fig. 11). Although these extensions and increases in area of the island are primarily due to marine currents, waves, and wind, the rapid growth of strand plants, particularly *Uniola* with its long, sand-binding rootstocks, aids materially in stabiliz-

ing the sands. *Suriana* bushes become scattered over the areas dominated by grasses and herbs, and soon replace them. Later the *Suriana* bushes die or are burned out and are replaced by *Chamaesyce*, *Opuntia*, *Agave*, and other plants of the dry-area communities described above. The rapid spread of *Casuarina* over these areas will probably lead to the development of an Australian pine forest. In any event, the gradual extension of the island by currents will continue to lead to the sequence of communities described above, and what will finally become of the areas once dominated by *Suriana* is a question.

Garden Key

History and topography. Most of this island (fig. 12) is occupied by Fort Jefferson, a six-sided brick structure about half a mile in perimeter, with walls 45 feet high and 8 feet thick (pl. 5, fig. 1). The small areas of sand outside the fort have shifted about and been variously disturbed during the long period of its building and occupancy, and have been affected by dredging operations in the channel around about half the perimeter of the island. For these reasons the vegetation and topography of Garden Key have been too much influenced by man to be considered as significant as those of the other islands.

The history of the fort itself is very interesting. In 1825 a lighthouse was erected on Garden Key, and in 1846 the construction of the fort was begun with slave labor. During the Civil War the slaves were replaced by military prisoners. After 1866 little work was done on the fort, as the invention of the rifled cannon made the structure obsolete. The major epidemic of yellow fever during 1867 and the work of Dr. Samuel A. Mudd in this connection are a well known story. In 1876 the post was abandoned, but it was used again and further developed during and after the Spanish-American War. In 1901 the U. S. Navy began construction of the two coal sheds and two piers and also began dredging the channel. The drawings of this construction show it as completed by July 1905; at that time dams at the ends of the coal sheds and in other places kept the sands from spreading into the 14-foot-deep channels between the sheds and piers. Since that day sand has filled in much of this area and the piers have nearly rusted down. Some dredging was done on Bush Key, east of Garden Key, that probably altered the shape of the latter. The fort was abandoned by 1910, but was used again as a seaplane base and wireless station during the First World War, being abandoned again in 1925.

Finally in 1935 the area of the Tortugas islands and particularly the fort were declared a national monument. Since that date the National Park Service has administered the area, and has cleaned up the fort and made it a beautiful show place. The Park Service has tried to preserve natural plants as much as possible and has encouraged the bird life in the area.

The island was probably lower originally than it is at present, as is indicated by the fact that a number of low places in the parade ground have been filled in. The fort and the buildings around it no doubt stabilized the island, and the changes that have taken place have consisted mainly in shifting and small increases in size of the sand areas outside the moat wall. There are two of these areas, one extending toward the northeast and the other toward the southwest coal sheds and docks. They cover about 5 acres, and the fort about 11, making the total area of the island about 16 acres.

Vegetation. The sand areas outside the fort, the parade ground inside, and the sand and coral debris on top of the walls and buildings all have distinct kinds of vegetation. That of the parade ground is entirely the result of cultivation, plantings, and care. The top of the fort has a number of plants that can grow in very dry and loose soils. This is a natural vegetation, but only on the sand areas outside the fort are the natural plant communities of this region developed, and these have been somewhat altered by the inhabitants of and visitors to the fort. So many exotic species, brought in as weeds or for ornamental and fruit purposes, have been added to the flora that it has become very diverse. Most of these exotic plants are listed in table 7, above.

The low sand areas outside the fort are so often shifted about that the establishment of plant communities as stabilized and mature as those on Loggerhead Key is prevented (pl. 5, fig. 2). In spite of this condition, four fairly distinct communities can be recognized. The largest of these is the *Uniola* strand-beach associates covering about half of the southwestern sand area, and *Uniola* with some of its common associates covering much of the sand area to the east of the fort. No large *Suriana* consocieties exist as on Loggerhead Key, but there are a number of colony groups of *Suriana* on the east side of the fort that are increasing in size and may be forming such a consocieties. *Sesuvium* forms a distinct consocieties above a wide beach between the northeast coal shed and the northeast wall of the moat; *Sesuvium* also covers most of the upper beach along the eastern sand area. A large area on the highest and driest part of the southwest sand area is covered by a very modified type of *Chamaesyce* associates with many weed species associated. In this area are a number of scattered individuals and patches of *Opuntia*, *Iva*, *Sporobolus*, *Cenchrus*, *Cyperus*, *Chloris*, and *Melanthera*. In addition to these, some of the weed plants, as *Valerianoides*, *Leptilon*, and *Boerhaavia*, are present in this associates and to a less extent in the *Uniola* associates. On the coarse sands and coral fragments filling in the northwestern moat *Tournefortia*, *Uniola*, *Sesuvium*, and *Suriana* have all begun to grow as pioneers.

The relatively poor development of a *Suriana* consocieties indicates that the vegetation is younger than on Loggerhead Key. On the sand areas out-

side the fort *Sesuvium*, *Uniola*, *Cyperus*, *Tournefortia*, *Scaevola*, *Ipomoea*, and other strand-beach and strand-dune plants are more common than *Suriana*, *Opuntia*, *Chamaesyce*, and other species of drier and usually less saline soils, a fact which indicates that these sands have shifted about, probably for a long time.

The plants growing in the coarse, dry coral and sand piled on the top of the fort are an assemblage of weeds and some native strand plants, all of whose seeds have been carried thither by winds, birds, or man. They receive little or no salt water, and this only during the infrequent great storms. Nevertheless a number of them are strand plants ordinarily associated with some soil salinity. Their growth here shows that a dry habitat is probably as important as salinity in the development of xeromorphic adaptations. The commonest of these plants are *Leptilon*, *Opuntia*, *Melanthera*, *Canavali*, *Cenchrus*, *Valerianoides*, *Sporobolus dominicensis*, *Ipomoea*, *Chamaesyce*, *Boerhaavia*, *Bidens*, *Poinsettia*, *Chloris*, *Paspalum*, *Digitaria sanguinalis*, *Eragrostis amabilis*, other grasses, and some good-sized bushes of the gumbo limbo tree, *Elaphrium Simaruba*. Many of these plants grow on top of the powder magazines inside the enclosures as well as on the top of the fort. No plant communities of any size are formed, but localized patches of some of the species form families and colonies of very limited extent.

On the parade ground and the lawn to the south of the fort, grasses, mostly *Cynodon dactylon*, the Bermuda grass, have been encouraged to form a lawn. The weed legume *Sesbania macrocarpa* that used to be common has now been removed except for a small patch outside the fort on the east side. *Hymenocallis*, the spider lily, has been planted or encouraged. The other plants are the shade and ornamental trees, fruit trees, and some weeds. The commonest tree is the native buttonwood, *Conocarpus erecta*. Some of these trees are as old as the fort, and have survived fires and wanton destruction of other plants and property. The probable origin of some of these buttonwoods was near or around depressions of the part of the original island that is now the parade ground. Other, younger buttonwoods have been planted or encouraged to grow since the fort was built. The silky-leaved variety, *Conocarpus erecta* var. *sericius*, is present, and was probably brought to the island from Key West, as it is common there. On the other hand, it may have arisen as a mutation on this island, as Bowman (1918) suggests.

Old pictures of the parade ground and the buildings of and about the fort show that a row of large coconut palms was growing in front of the officers' quarters and near the north powder magazine in 1898. At that time there were definite paths between the then more numerous buttonwood trees on the parade ground, and many smaller ornamentals were planted along these paths. At one time there was a garden enclosure. Since the fort has

been made a national monument, more coconut trees have been planted, and no doubt other ornamentals will be added.

The other larger and older trees and shrubs are *Tamarindus indica*, the tamarind; *Phoenix dactylifera* and *P. canariensis*, date palms which both bear edible fruits in this dry location (pl. 5, fig. 1); *Thespesia populnea*; *Elaphrium*; *Cordia sebestena*, the geiger tree, with beautiful orange-red flowers; a number of oleander bushes; and the native sea grape, *Coccolobis uvifera*. Both *Agave americana* and *A. sisalana* were planted or encouraged to grow. The guava, *Psidium guajava*, and other plants have been added recently. A few *Casuarina* trees were planted here, but have not been allowed to become naturalized as on Loggerhead Key.

Clearing and improvements outside as well as inside the fort will probably reduce the natural vegetation, and if the island is improved by plantings not much of the natural vegetation will remain.

Bush Key

Topography. More changes have occurred in both the topography and the vegetation of Bush Key (fig. 13) than in any other of the now existent Tortugas Keys. Lansing evidently found so little sand above the wash of the waves in 1904 that he gave no account of the island to Millspaugh. In 1915 Bowman found both *Suriana* and *Tournefortia* bushes about 12 years old, which probably indicates that Lansing overlooked the small island in 1904. Certainly some of it was there prior to 1900, as at that time the U. S. Navy removed sand from the island to make improvements at the naval base on Garden Key. The dates of this dredging were about 1901-1905, but the extent of the changes caused by it is not known.

Whatever the conditions prior to 1900, the small remnant of the former Bush Key has now grown to be an island (pl. 6) as large as Garden Key. During this 40-year period two narrow ridges of sand and broken coral enclosing a lagoon have gradually grown together, most of the lagoon has filled in, and a spit has extended far to the east, almost connecting the main body of Bush Key with the coral-fragment shoal and bar of Long Key. This rapid growth was probably a restoration of some of the parts of the island removed before 1905.

The different shapes that the island has assumed during this period are hard to ascertain. Bowman's map and some of the descriptions by others do not seem to be very accurate. The U. S. Coast and Geodetic Survey charts do not show the island as anywhere near so large as it has been for many years. Bowman's drawing seems to be inaccurate as to compass direction, for when it is compared with a present-day map, it is only possible to make the two coincide by assuming a shift of about 90° in the compass indicator on his map. He shows the long bar of the island as extending almost due south, whereas at present it extends only a few degrees south of east.

As the two sand ridges of Bowman's day, 1915, grew together, the island also extended farther west toward Garden Key, until now its sharp western point is on the very edge of the deep channel between the two islands (fig. 12). The eastern sand ridge has also been extended. The present diamond-shaped main part of the island is mostly the result of the coalescence of the northern and southern ridges, and the filling in of the lagoon that lay between them. Some of the lagoon was dredged out before 1905, and it quickly filled in. The present ponds and the low areas around them represent its remains. Pearse (1934) observed these ponds in 1931, and says, "Dr. Paul Bartsch, who had visited Dry Tortugas annually for a long period, states that the ponds were cut off from the ocean about 1919." This was soon after Bowman's visits. The filling in of the ponds (see fig. 13) has now progressed until pond 2 is very shallow, about 6 inches, and pond 1 is not over 18 inches deep in any part. The bottoms and margins of both ponds are of a muck soil formed from a combination of calcareous sediments and organic remains of plants and animals. Pond 3 is a very small pool, containing only temporary rainwater. Because of the mode of its formation, the central parts of the island are in most places lower than the periphery. The highest parts are not over 3 feet in elevation.

The present area of Bush Key is about 19 acres, whereas Bowman's drawing shows an area about half as great. Since the area of Garden Key and the fort is about 16 acres, Bush Key has outgrown Garden Key in recent years. Bush Key will probably continue to grow, but more slowly, as its size and shape are now about stabilized. A gradual decrease in area is possible if the birds denude the island of too much vegetation and erosion destroys parts of it.

Vegetation. Bush Key during its rapid growth of the past 40 years has developed a very mixed vegetation. The strand communities are small, consisting mostly of consociates, colonies, families, and scattered individuals, so that it is difficult to give a general description. Unlike Loggerhead Key, with its relatively well defined vegetational units, this island has few distinct communities. Much of the island is similar to the upper beach and fore dune, with such plants as *Sesuvium*, *Sporobolus*, *Ipomoea*, *Uniola*, and *Tournefortia* scattered over nearly any part of it.

Suriana has formed only a few patches large enough to be considered a *Suriana* consociates. There are only a few patches of *Opuntia*, and they form no distinct community. The *Uniola* strand-dune associates and the *Chamaesyce* associates cover the largest areas. Between these associates, in them, and around the upper part of the beaches occur some of the plants of the strand-beach associates. Most abundant of these is *Sesuvium*, which here covers such large areas that a distinct *Sesuvium* consociates is recognized (pl. 7, fig. 1). *Tournefortia* is scattered over much of the island. Large patches of *Iva*, *Scaevola*, *Sporobolus*, and *Chloris* form fairly distinct socias.

Around the ponds are three distinct communities. Around pond 1 is a thick stand of white mangroves with a few red mangroves, forming a *Laguncularia* associates. Outside this mangrove zone, over the damp muck soils, is a very distinct *Alternanthera* society which also grows around part of pond 2. Around pond 3 is a thicket growth of buttonwood. Some red mangroves have been planted around pond 2 and may grow to form a colony.

The drier parts of the island are made up largely of coral fragments, with some coarse sand. On this dry soil a *Chamaesyce* community, with scattered patches of other plants in it, has developed. Nearly bare areas are increasing as *Suriana*, *Sesuvium*, and other plants are killed by the nesting of the thousands of terns that have moved here since Bird Key became submerged. As was the case with Bird Key, this destruction may mean the beginning of the end of the vegetation and finally of the island itself.

Long Key

Topography. Long Key is here considered to be only the coral-debris bar (fig. 13) that lies southward from the eastern terminus of the long sand ridge extending eastward from the main part of Bush Key (pl. 6). Long Key is in two parts separated by a shallow channel. The northern part is small and is connected at low tide with the eastern extension of Bush Key. Both parts are over one-third covered by the high tide, and the highest mounds of coral debris are seldom over 2 feet above high water. Some calcareous sand has accumulated with the coral fragments, and finer sands and muds occur in the shallows around the bar. Storm waves sweep completely over the bar, so that no sand areas have as yet developed and the coral fragments and plant life are probably completely or partly covered by water a number of times a year.

The long southern part of this bar seems to be extending southward. It is increasing in size as coral debris is piled up by the waves. The shallow embayment between this bar and the eastern shore of Bush Key is filling in. It seems probable that the two keys may eventually become joined. Sands are accumulating on top of some of the coral debris, and a sandy strand island may develop.

Vegetation. The vegetation is sparse, covering less than one-third of the area above mean high tide. It consists of scattered individual plants of *Rhizophora* and *Avicennia*, with patches of the salt-marsh plants *Salicornia* and *Batis* and the strand-beach plant *Sesuvium*. In most cases these patches are pioneer families of one species, but in some cases there is a colony of two or more species.

Many seedlings of *Rhizophora* have taken root between the coral fragments. The total number of these in 1938 was 187, of which only 11 had the number of leaves, leaf scars, or branches of the average plant over 4 years old. This indicates that few of these plants survive beyond a stage of

primary growth from nutrients furnished by the seedling. Most of them take root between low-tide and high-tide levels.

In 1937 a few *Rhizophora* seedlings were planted. In 1938 a total of 4100 were planted, and about 3300 of these had survived in August 1940, when 575 were added. In February 1942 over 2500 of these had survived. Many of these were planted offshore in deeper water than that in which seedlings could normally become rooted, and they were doing well even though submerged by the tide (pl. 7, fig. 2). The high percentage of survival over 3½ years indicates that these plantings may grow well and establish a mangrove swamp. If this occurs, the whole character of the island will change. More sediments and sand will collect, the coral debris will be covered by sand, and eventually an island of more stability and higher elevation will be formed. The plantings were made to see if just such a change could be promoted. If so, then we may have a clue to the probable mode of development of some of these Tortugas islands. Parts of Bush Key were most likely developed in this manner.

Only a few *Avicennia* bushes grow on Long Key. In 1940 there were 25, of which 4 were over 2 feet tall. They have established themselves on or near the highest mounds of the coral ballast. No plantings were made of *Avicennia*, but most likely it and *Laguncularia* will both become associated with the *Rhizophora* bushes if a swamp develops from the plantings of the latter.

Salicornia forms many patches, most commonly over the areas of intermediate elevation, and *Sesuvium* slightly smaller areas, usually at the highest elevation. Only one small patch of *Batis* associated with *Sesuvium* was present in 1940.

Sand, Middle, and East Keys

Topography and vegetation. These three islands are so small that their shape has changed and one of them, Middle Key, seems to have an intermittent existence. Millspaugh described no plants from it, but it was a small sand island in 1904. In 1915 and 1916, Bowman found on Sand Key only a few plants less than were found by Lansing; only *Cakile* was found on Middle Key, and most of East Key was covered with vegetation. Thus of the three only East Key, the largest, has had a consistent vegetation, parts or all of the other two islands having been awash in rough weather from time to time, so that the plants were destroyed.

Middle Key was a low, crescent-shaped island about 75 feet long in the summer of 1937, and only a few individual plants of *Cakile*, *Iva*, and *Chamaesyce* grew on it. A little sand was visible at the neap tide in July 1938, but none was noted in 1940 or 1942.

Sand or Hospital Key was about 110 by 70 feet in 1938; some of the sand above 2 feet in elevation supported a few strand-dune plants, mostly *Uniola*,

Tournefortia, and *Chamaesyce*, none of which had been noted by Bowman. Some indurated beach rock, and piles of brick left from the small hospital built here in the 1870's, indicate that the island has been fairly stable. It has increased in size and vegetation since 1915.

East Key is about 4.2 miles east-northeast of Garden Key, and from the records seems to have been of about its present size for the past 60 years. It has had a good vegetational covering since 1904. The plants noted by Millspaugh and later by Bowman did not include any *Suriana* bushes, which are now forming a thicket growth along the highest part of the dune plateau. Most of the vegetation is a *Uniola* strand-dune associates. *Ipomoea*, *Sesuvium*, *Cenchrus*, and other strand-beach plants are present on the upper beach. Since the island is much larger, about 1200 feet long by half as wide, than the others of these three islets, and since its dune plateau has an elevation of 3 feet and a vegetation developing toward the *Suriana* con-societies type, it has probably grown in size and become more stabilized in the past half-century, in contrast with the intermittent history of the two other islands.

SUMMARY AND CONCLUSIONS

About thirty islands of the Florida Keys beyond Key West were investigated during the summer of 1940 and winter of 1942, and to some extent during the summers of 1937 and 1938. These studies were concerned with the topography and vegetation of these small, relatively isolated, and partly tropical islands. The probable modes of formation of the islands, their topography and topographic changes, the vegetation, and the successional relations of the plant communities of which it is composed were the particular concern of the investigation.

These thirty-odd islands are in three main groups. Ten extend west from Key West to Boca Grande Channel. These are low islands, many of them covered only by mangrove swamps, and are based on an oölite limestone rock which is an extension of the rock that forms the islands of the lower Florida Keys. The second group consists of ten or more islands arranged in an elliptic atoll, named the Marquesas Keys. This atoll is based on the same oölite limestone; it was and is being formed by definite currents which cause the accumulation of detrital materials, coarse calcareous sands, and muds. The third group is the well known Tortugas Keys, now consisting of six islands but formerly of eight. Coral reefs and banks surrounded by deep water, together with the islands, form a partly completed elliptic atoll similar to the Marquesas Keys and seemingly built up by the same agencies. The Tortugas islands are composed almost entirely of coarse calcareous sands. There have been enlargements of some of the islands and complete or almost complete destruction of others at both the Tortugas and Marquesas atolls.

These islands are here termed the Sand Keys because most of the parts above high tide are composed of coarse calcareous sands, and also because this name was used by Millspaugh (1907) in his description of them. Bowman (1918) described some of the topography and all the vegetation of the Tortugas Keys, and these two descriptions with a number of other publications about this region furnish fairly good bases for comparing past with present conditions, so that topographic and vegetational changes can be determined.

The vegetation consists of mangrove swamps with a few salt marshes, and abundant strand vegetation on the elevated sandy parts of the islands. Both of these types of vegetation are arranged in fairly definite zones of plant communities, which form two successional series, the mangrove sere and the strand sere. Most attention was given to the strand communities, as the details of mangrove swamps had been previously studied (Davis, 1949). The strand succession consists of four fairly distinct stages, well represented on these islands as a whole but only partly developed on some of them. The mangrove succession consists of two main communities, which are less well developed than the mangrove swamps of much of the southern Florida coast.

The flora in general, the plant populations of the particular communi-

ties, and some details of the mode of dispersal of the plants are considered. The relatively small number of species, the wide distribution of certain pantropic species, and the dispersal of some of these by water, birds, wind, and man are of special interest.

The most effective environmental factors are salinity, soil moisture, coarseness of the strand soils, rainfall, relative elevations of the mangrove and strand soils, and depth of inundation. The strand soils are so coarse and the rainfall so sparse during six months of the year that most of the strand communities are very xeric. Soil moisture most affects the strand communities. Salinity affects only the pioneer strand community. Salinity and depth of inundation most affect the mangrove communities.

The adaptations of the plants to both dryness of the sand soils and salinity of the swamps, marshes, and fore dunes express themselves in numerous xeromorphic features of anatomy and form, particularly of the leaves.

After the topographic, vegetational, floristic, and environmental features of the islands have been considered as a whole, a detailed description of each island is given, covering the topographic and vegetational features and the relations between the two. Particular emphasis is placed on the changes in topography and the plant communities that seem to have taken place, especially since the studies by Millspaugh and Bowman. A few of the Marquesas and Tortugas keys have changed a great deal. The strand areas on a number of islands seem to be increasing at the expense of the mangrove swamps, as a result of accretion of sand. The mangrove swamps have spread over wide areas in some instances and seem to be aiding in building up the islands. Most of the constructional processes are, however, due to maritime factors such as the ocean currents and tides.

No two islands have identical plant communities. In general, the islands near Key West are entirely or mostly covered by mangrove swamps, and the sand areas increase westward until at the Tortugas Keys the vegetation of the islands consists almost altogether of strand plant communities, only a few mangroves and salt-marsh plants occurring around ponds and on a low island nearly awash at high tide.

The maps accompanying this report are drawn from field surveys made during 1940. They are in a number of instances quite different from those published by the U. S. Coast and Geodetic Survey, by Millspaugh, and by Bowman. Until more exact surveys can be made, these maps may be considered fairly accurate, and they show some important changes in recent years.

These islands should prove appropriate for a long-term study of insular changes, both topographic and vegetational. The present investigation adds to the information given by Bowman and Millspaugh and, it is hoped, will contribute to future studies.

This paper is also a part of a series of studies of the plant ecology of southern Florida. This and the author's study of mangrove vegetation together describe most of the coastal and insular vegetation of that region.

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FIG. 1. Mangrove swamps cover many of the tide-inundated parts of the islands. Here on Man Key the oölite limestone shows at low tide in a lagoon.



FIG. 2. The dune plateau is covered by a grass and herb vegetation, inland from which buttonwoods and mangroves grow on lower soils.



FIG. 1. *Tournefortia*, a sea lavender, is common along the edge of the dune terrace. It blooms in February.



FIG. 2. Large areas in the interior of Boca Grande Key are an oölite limestone plain. On the higher parts of the plain are scrubby hammock forests, shown in the distance.

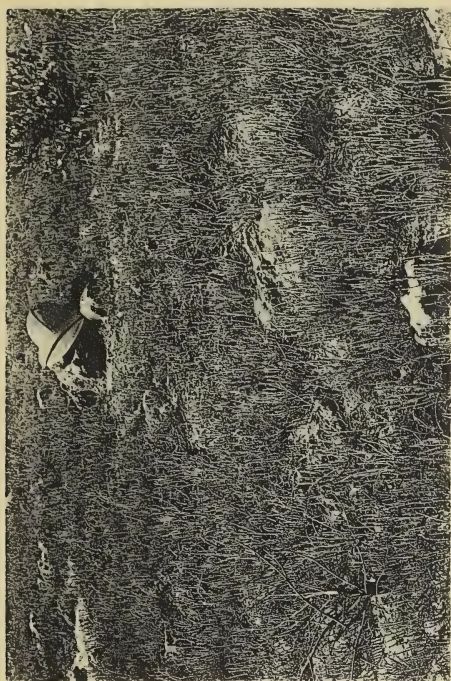


FIG. 2. *Salicornia*, the glasswort, and other salt-marsh plants cover the salt flats on Boca Grande Key.



FIG. 3. *Hymenocallis*, the pretty spider lily, grows well on the sand strands.



FIG. 1. View toward the northeastern end of Loggerhead Key, showing the path between the thicket growth of bay-cedar bushes, *Suriana maritima*. Note the many planted coconut palms, *Cocos nucifera*, and the tall growth of the introduced Australian pines, *Casuarina equisetifolia*, around the Carnegie Institution laboratory at the northeastern end.



FIG. 1. The orchid *Epidendrum tampense* blooms in the rock and strand hammocks in July.



FIG. 2. The century plant, *Agave americana*, has spread over many areas on Loggerhead Key.



FIG. 3. The prickly-pear cactus, *Opuntia Dillenii*, is replacing *Suriana* on many of the drier parts of the Tortugas Keys.



FIG. 1. Date palms (*Phoenix*) on the parade ground of old Fort Jefferson, on Garden Key, bear ripe fruit because the climate is dry. A never completed powder magazine and some of the casemates of the fort are shown.



FIG. 2. Outside Fort Jefferson the natural sand-strand vegetation is not in definite zones. Here the sea oats, *Uniola* (tall, plumelike), the sea rocket, *Cakile* (in bloom), and the bay cedar, *Suriana*, and *Tournefortia* (in background) all grow together.



View of diamond-shaped Bush Key from the top of Fort Jefferson; Long Key bar in background. Bush Key has been built up mainly since 1905.



FIG. 1. Typical *Sesuvium consocias*, in foreground, on Bush Key. Thousands of terns nest here, and bare areas are left from this summer nesting.



FIG. 2. Some of the survivors of planted red mangrove, *Rhizophora*, seedlings in the shallow waters near Long Key. These are 3 years old and are now so firmly rooted that they will probably survive all but severe storms and aid in enlarging the island.

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